A REVISION OF CERTAIN ACTINOPTERYGIAN AND COELACANTH FISHES, CHIEFLY FROM THE LOWER LIAS

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SYNOPSIS

A redescription of part of the fish fauna of the Lower Lias is given, supplemented by an account of relevant Upper Liassic, Triassic and Permian forms. This has involved a complete redescription of the majority of the Palaeoniscoid and Subholostean genera and of such Holosteans that have not previously been adequately described. The origins of the Holostei are investigated and it is concluded that they are of polyphyletic origin, at least three independently derived lines being recognizable within the group. The separate evolutionary lines within the Holostei are discussed and in particular that which leads through *Pholidophorus* to the Teleostei. A discussion is given of repeated parallel evolution within the various lines of Holostei.

I. INTRODUCTION

THERE are good modern accounts of a number of Triassic fish faunas. In the Lower Trias, marine faunas from Spitsbergen, Greenland and Madagascar have been described by Stensiö (1921, 1925, 1932) and Piveteau (1934, 1941), and freshwater faunas from Australia by Wade (1935, 1940, 1941). In addition, there are more recent accounts of faunas from the Lower Trias of Madagascar by Lehman (1952), from the Middle Trias of Besano, Lombardy by Brough (1939), and from the Lithographic Stone (Lower Kimmeridgian) of Cerin by Saint-Seine (1949). However, the rich fauna from the Lower Lias has received no modern comparable treatment.

The earliest descriptions go back to Egerton (1852) and were revised by Woodward at the end of the last century in the British Museum *Catalogue of Fossil Fishes*. More recently Rayner (1941, 1948) has redescribed several of the more important Holosteans and attempted a classification of the group.

England has produced the majority of the known fishes from the Lower Lias, Lyme Regis being by far the richest locality. Other localities include Watchett and Street, in Somerset; Stratford-on-Avon, Warwickshire; Barrow-on-Soar, Leicestershire; Bushley, Gloucestershire. Abroad, specimens come from Alsace-Lorraine, Würtemburg and a few other German localities. The main collection is in the British Museum (Natural History).

The fauna is large and well preserved. It includes Elasmobranchs, Chimaeroids, Sturgeons, Coelacanths, Palaeoniscoids, Subholosteans, and many Holosteans, which last form the bulk of the collections. The limy matrix in which the specimens are preserved makes possible the application of the modern technique of acid preparation (Toombs 1948; Rixon 1949).

The fauna is important as it throws light both on the origin of the Holostei and on the evolution, from the Holostei, of the present day Teleosts.

II. SYSTEMATIC DESCRIPTION

Order *PALAEONISCOIDEA*

Family Coccolepidae

Diagnosis. Palaeoniscoid fishes of slender fusiform shape with deeply forked, somewhat unequilobate tails. Fins of Palaeoniscid type, large, with the rays all articulated and branching distally; lepidotrichia far more numerous than supporting radials. Mandibular suspensorium oblique, dentition consisting of a set of regularly spaced, large teeth, interspersed with minute, sharply pointed teeth. Branchiostegal rays well developed. External skull bones generally ornamented with irregular tubercles and ridges. Fulcra minute or absent. Scales thin and deeply imbricating, ornamented with tubercles of enamel.

Genus ***COCCOLEPIS*** Agassiz, 1843

Diagnosis. As for family (only genus).

Type species. *Coccolepis bucklandi* Agassiz.

Remarks. The genus *Coccolepis* was founded by Agassiz (1843 : 300, pl. 36, figs. 6, 7) when he described *Coccolepis bucklandi*. Since that date eight other members of the genus have been described, *Coccolepis andrewsi, liassica, australis, macroptera, aniscowitchi, martynovi, cockerelli* and *socialis*, although Berg (1948 : 1243) considers both *C. socialis* and *C. cockerelli* to be synonymous with *C. aniscowitchi*. However, although the obvious Palaeoniscid affinities of the genus were recognized at an early date, there has been no adequate description of any of the individual species. With this in mind I have undertaken a re-examination of the species *Coccolepis liassica*.

Coccolepis liassica Woodward

(Text-figs. 1, 2, 4)

1890. *Coccolepis liassica* Woodward, p. 432, pl. 16, figs. 2–4.
1891. *Coccolepis liassica* Woodward : Woodward, p. 525.

DIAGNOSIS. A *Coccolepis* of moderate size, length of head contained about four and a half times in total length and equals the maximum depth of body. External skull bones strongly ornamented with rounded tubercles and a few ridges. Subopercular deeper than broad, larger than the opercular.

SYNTYPES. B.M.N.H. P 887, P 6153 and 39865 from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H.

DESCRIPTION. *The skull.* The general shape of the skull can be seen from Text-fig. 1. The snout is rounded with the orbit lying well forward. The relatively large nasal orifice is situated more ventrally than in the majority of Palaeoniscids. The external bones of the skull are all ornamented with enamel, and so in life were not covered by soft tissues. The ornamentation of the skull roofing bones consists of pronounced coarse tubercles, which in places give way to a more rugose structure. A similar somewhat finer ornamentation covers the nasal, postrostral and preopercular. The maxilla is characterized by lines of tubercles which occasionally anastomose into ridges. The supraorbital and infraorbital bones have barely any

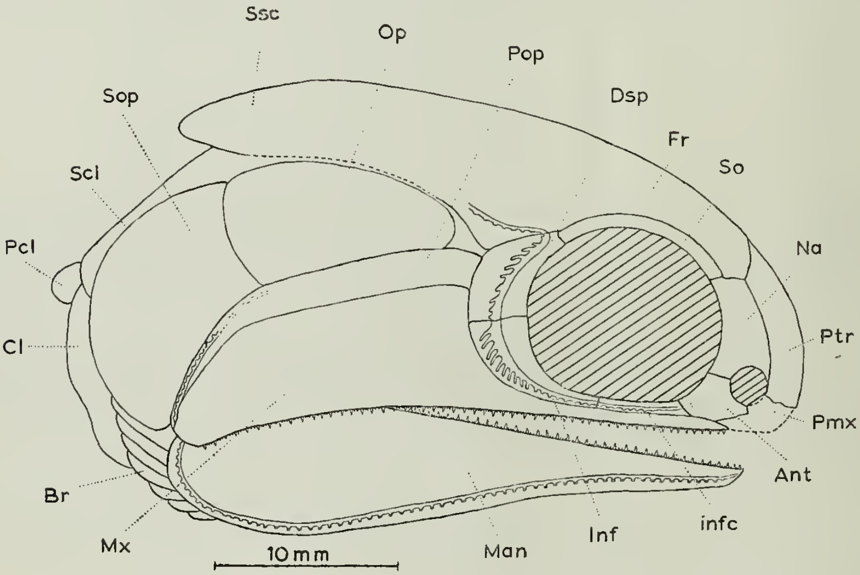

FIG. 1. *Coccolepis liassica* Woodward. Restoration of skull in lateral view.

ornamentation. The ornamentation of the opercular and the subopercular shows numerous coarse striae which run concentrically around the bones, whilst the branchiostegal rays also exhibit similar concentric striations. The mandible is much more coarsely ornamented than the skull bones, and has a pronounced mandibular sensory canal running along its length. The passage of this canal is marked by a series of pits which open to the exterior.

All the specimens of *Coccolepis liassica* are laterally crushed and consequently the demarcation of the individual skull roofing bones is difficult to interpret. Only in the anterior region can suture lines be made out with any degree of certainty. The frontals constitute the major portion of the skull roof, and anteriorly they meet the postrostral and nasals. The postrostral is a large bone whose general shape can be seen in B.M.N.H. P 11772. It extends downwards to form the rostrum and on either side it joins the nasal along most of its length. Posteriorly the nasal borders a considerable portion of the orbit ; dorsally it abuts against the supraorbital and ventrally the antorbital. In its antero-ventral corner the nasal has a pronounced semicircular notch, this forms part of the border of the nasal orifice. The antorbital is of a roughly triangular shape and limits the orbit behind and the nasal orifice in front. No trace of a premaxilla could be found, but from the general shape of the bones in the anterior region there is reason to believe one existed. It must have adjoined the antorbital and the maxilla posteriorly and the postrostral dorsally. The other bones limiting the orbit are the infraorbitals beneath and behind and the supraorbital above. The most anterior infraorbital is a narrow bone extending back along the dorsal margin of the maxilla from the antorbital to the next infraorbital. The second infraorbital is narrow anteriorly, but as it extends upwards it broadens considerably. From the infraorbital a broad dermosphenotic limits the remainder of the posterior edge of the orbit. The dermosphenotic is connected to the infraorbital by a straight suture and ventrally rests in the concave anterior margin of the maxilla and the preopercular. Running through the surface of the dermosphenotic and the infraorbitals is the intraorbital sensory canal. As this canal traverses the dermosphenotic and the succeeding infraorbitals it gives off numerous fine branches posteriorly. These can be seen on B.M.N.H. P 11772. Along the lateral edge of the frontal and bordering the orbit above is the single supraorbital bone.

The maxilla is of the normal Palaeoniscid pattern, much broadened posteriorly and long and slender anteriorly. Its oral border is completely lined with teeth, right back to its extreme posterior angle. The teeth are in two series, the larger, regularly spaced, slender and slightly curved teeth interspersed with minute, sharply pointed teeth. The preopercular is very much smaller than the maxilla, to which it is attached along the whole of its length, forming almost a cap to the latter bone. The preopercular sensory canal can be traced part of the way along its posterior border. The suspensorium is very oblique, as can be observed from the angle of the opercular bones. The opercular itself lies almost horizontal above the dorsal edge of the preopercular. There is no evidence of any other bones between these two elements corresponding to the " dermohyal " of Moy-Thomas & Dyne (1938 : 441) or to the bone " X " of Traquair (1901 : 83). The subopercular is more vertical in position, deeper than broad and larger than the opercular. There are fifteen branchiostegal rays on each side, broadened anteriorly and delicately ornamented with concentric striations. The gular plate is relatively small in this species and it is similarly ornamented to the branchiostegal rays. The lower jaws are stout and bear numerous teeth along their posterior margins. The dentition is similar to that of the maxilla with two series present. The teeth of the larger series are somewhat stouter than the corresponding ones found in the maxilla. Of the other skull bones little can be made out.

Appendicular skeleton. The pectoral girdle is not complete in any of the specimens, but its general form can still be ascertained. The supracleithrum is a wide bone stretching from the expanded suprascapular to midway down the subopercular. Here it joins a somewhat reduced cleithrum. A small almost circular postcleithrum is also present. The fin itself is small with between eighteen and twenty lepidotrichia. The rays are distally dichotomized and distantly articulated. The fin has a narrow insertion and there are no fulcral scales present.

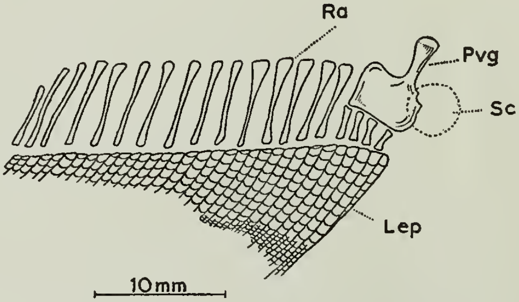

FIG. 2. *Coccolepis liassica* Woodward. Girdle and supporting structures of the pelvic fin. From B.M.N.H. P 3697 and P 894.

The structure of the pelvic fins and girdle can be seen on B.M.N.H. P 894 and its counterpart P 3697 (Text-fig. 2). Internally there is a paired skeletal structure of rather unusual form, consisting of an almost square plate with a projection from its antero-dorsal corner. This projection meets that of its opposite member to constitute the pelvic girdle. Immediately below this paired structure are four reduced radials and posterior to it another fifteen longer radials, making nineteen in all. From the radials arise twenty-nine lepidotrichia which make up the pelvic fin. The base line of this fin is extended and the fin arises slightly to the anterior of the dorsal fin, midway between the pectoral and anal fins. The fin is triangular in outline, with all the rays articulated and branching distally.

Unpaired fins. The dorsal fin (Text-fig. 3) arises at the middle point of the back opposite the posterior half of the pelvic fin. The fin is distinctly triangular, similar in outline to the anal, but with a shorter base. There are between twenty and twenty-five lepidotrichia, which increase in length up to the fifth, and then decrease in length as they pass backwards. A typical diamond-shaped fulcral scale was observed at the anterior end of this fin, in contrast to the statements to the contrary by previous workers (Woodward, 1891 : 523). Supporting the dorsal fin is a series of endoskeletal supports, but since the material was poorly preserved in this region, examination of another species was necessary to obtain a clear picture. A specimen of *Coccolepis andrewsi* (B.M.N.H. P 6302) shows a beautifully preserved dorsal fin, from which I have drawn Text-fig. 3. There are approximately nineteen of these endoskeletal supports, long and rod-like in general shape and expanded at their articulation with the fin rays (numbering twenty-nine to thirty in *Coccolepis liassica*). Beneath these endoskeletal supports the neural arches are reduced, the neural spines being absent.

The anal fin (Text-fig. 4) is similar to the dorsal with twenty-five lepidotrichia all distally dichotomized. There are between twelve and thirteen endoskeletal rods supporting the fin (B.M.N.H. P 11772). They are of the same general shape as those of the dorsal, perhaps a little more expanded at their articulatory points with the fin rays.

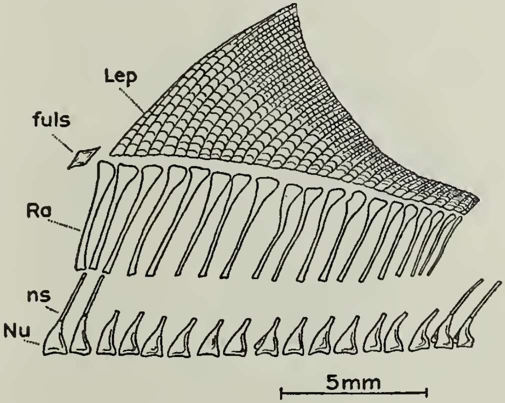

FIG. 3. *Coccolepis andrewsi* Woodward. Reconstruction of dorsal fin. From B.M.N.H. P 6302.

The heterocercal tail is deeply cleft with the upper lobe slightly the longer. There appear to be about forty-one fin rays of which the principal rays of the lower lobe are the stoutest. The fulcral ridge scales are well developed along the upper lobe of the tail, being arranged in six to seven rows with approximately twelve scales in each row.

Axial skeleton. The notochord was persistent since there are no traces of ossification in the notochordal sheath. The neural and haemal arches which bound the space occupied by the persistent notochord, are present along the whole length of the fish. The neural arches anterior to the dorsal fin bear long neural spines, which are not fused to the supporting arches, but remain quite distinct. These spines are missing in the area of the dorsal fins, but more posteriorly in the caudal region they are again present, although fused completely with the rest of the neural arch. Anteriorly the haemal arches are much reduced, bearing no spines. The arches become stouter in the caudal region (just anterior to the anal fin) and have long haemal spines. The most posterior haemal arches are elongated and distally thickened for the articulation of fin rays in the lower lobe, whilst the upper lobe rests on a series of slender rods which are in all probability neural spines.

Squamation. Very few of the specimens exhibit scales, but one or two isolated flank scales are visible on P 4370*a*. These scales are cycloidal in form and each divided into two distinct areas. The more anterior, overlapped portion is ornamented by fine concentric lines, but the ornamentation of the exposed area is more elaborate, consisting of lines of tubercles horizontally arranged with occasionally some of the tubercules fusing into ridges. There appear to be fulcral scales only in front of the dorsal fin (one ridge scale being recognized) and on the upper caudal lobe. Here the scales are more diamond-shaped, smooth and arranged in six to seven rows along the length of the lobe.

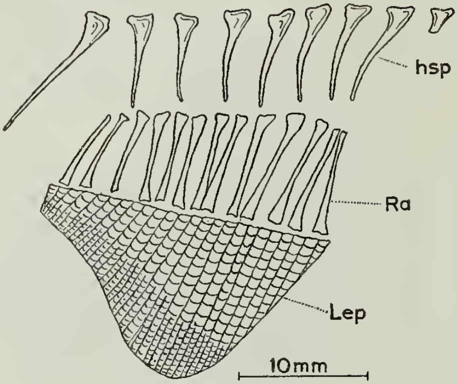

FIG. 4. *Coccolepis liassica* Woodward. Reconstruction of anal fin, mainly from B.M.N.H. P 11772.

Family CENTROLEPIDAE

DIAGNOSIS. Palaeoniscoid fishes of moderate size, fusiform shape and elongate bodies, with the maximum depth of the trunk equalling the length of the head, and contained almost four times in the total length. Opercular twice as long as broad, and a little larger than the preopercular. Two suborbitals present. Fins large and of the Palaeoniscoid type, with stout, flattened rays, all articulated and distally bifurcating ; anteriorly fringed with well-developed fulcra. Mandibular suspensorium oblique, dentition consisting of an inner series of large, widely spaced teeth, an outer series of more closely set, much smaller and sharply pointed teeth, and a shagreen of small rounded denticles on the coronoid, palate and branchial apparatus. External skull bones ornamented with tubercles and ridges of enamel. Form of the tail unknown. Scales thick and highly ornamented with serrations, ridges and furrows.

Genus **CENTROLEPIS** Egerton, 1858

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. *Centrolepis aspera* Egerton.

REMARKS. The genus *Centrolepis* contains only one species, *Centrolepis aspera*. Woodward (1891 : 521) classified it with the Palaeoniscids, mainly on the character of the skull roofing bones. Later Romer (1945 : 580) placed *Centrolepis* under the heading Palaeoniscoidea or Subholostei *Incertae Sedis*. It is shown below that the genus correctly belongs with the Palaeoniscoidea as Woodward (1891) anticipated.

Centrolepis aspera Egerton

(Text-figs. 5–12)

1844. *Centrolepis aspera* Agassiz, 2, pt. 1, p. 304.
1858. *Centrolepis aspera* Egerton, no. 5, pl. 5.
1890. *Centrolepis aspera* Egerton : Woodward, p. 430, pl. 16, fig. 1.
1891. *Centrolepis aspera* Egerton : Woodward, p. 521.

DIAGNOSIS. As for family and genus (only species).

HOLOTYPE. A well-preserved laterally crushed specimen in the B.M.N.H., represented by P 582 and the counterpart P 3510. Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H.

DESCRIPTION. *The skull.* The skull of *Centrolepis* is long, with a very oblique suspensorium and the orbit situated well forward (Text-fig. 5). The suprascapulars, frontals and parietals are covered with small symmetrically placed tubercles of enamel, which on the nasals and postrostral give way to raised ridges of enamel which run along the length of the bones. The small portions of the infraorbital series (B.M.N.H. 38123) which can be distinguished show a tubercular pattern, whilst the two members of the suborbital series have ridges of dentine similar to those of the nasals. The maxilla exhibits vertical striae near its ventral border, but these soon break up into separate tubercles so that the major portion of this bone and the preopercular have an ornamentation similar to that of the roofing bones. The ornamentation of the opercular is somewhat different, consisting of rows of tubercles running along its length with distinct grooves in between the separate rows. A similar pattern is to be found on the subopercular, but here the rows and grooves run more concentrically round the bone. The branchiostegal rays are coarsely tuberculated, while on the mandible stout ridges or striae run more or less along its length.

The few specimens belonging to this species are all laterally crushed, thereby making the interpretation of the skull roofing bones very difficult. The posterior extremity of the skull is covered by a distinct suprascapular from beneath which appears the large supracleithrum. The parietals and frontals are both large and constitute the major portion of the skull roof with the dermopterotics considerably extending its lateral borders. Anteriorly the frontals meet the nasals and postrostral. The postrostral abuts on the nasal along its entire posterior edge except where the external nares occur. The postrostral forms the anterior edge of the orifice and the nasal the posterior, much as in many of the Palaeoniscoids described by Moy-Thomas & Dyne (1938). Posteriorly the nasal borders the orbit and dorsally articulates with the frontal and supraorbital. Ventrally it joins the rostralo-premaxillary. From B.M.N.H. P 5594 the internal structure of the nasal and the postrostral can be seen (Text-fig. 6). On the inner surface just posterior to the nostril there is a bridge of bone on the wall of the nasal, a structure of which there is no previous account in the literature. It is obviously part of the nasal passage but its significance is not apparent. Also, on the inner surface a series of circular pits occurs in the bone (Text-fig. 6). The main infraorbital sensory canal round the snout does not split into two branches while in the rostral-premaxillary, as in most of Moy-Thomas & Dyne's illustrations (1938), but divides into two in the nasal, the main branch continuing up round the nasal and on to the frontal, while the smaller branch passes into the postrostral. It seems probable that the bone I have termed nasal represents two elements, the nasal and the antorbital which have become fused. The rostralo-premaxillary, the internal surface of which can also be seen on P 5594, articulates with the nasal dorsally, the infraorbital posteriorly and the maxilla ventrally. It forms a small portion of the border of the orbit and does not appear to bear any teeth. The infraorbital series comprises two bones which border both the lower rim

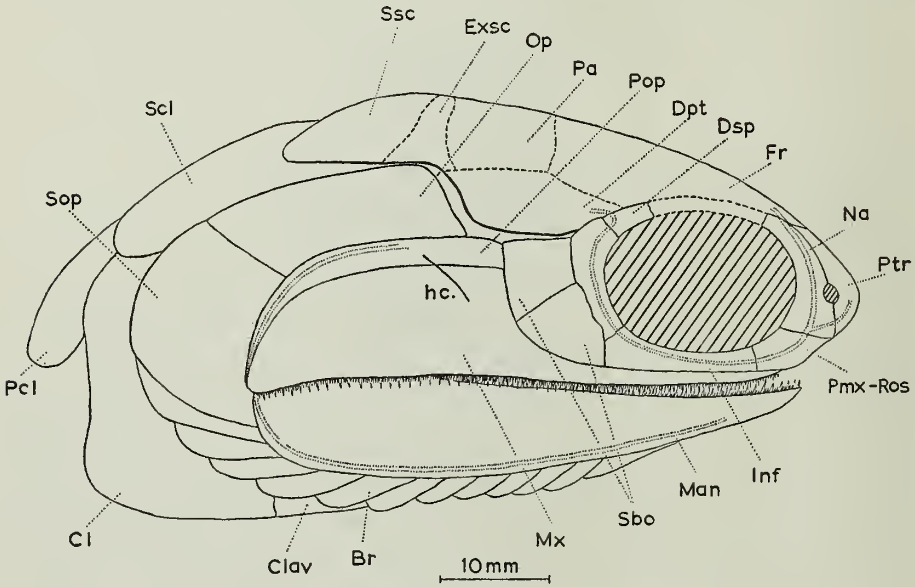

FIG. 5. *Centrolepis aspera* Egerton. Reconstruction of skull in lateral view.

of the orbit and its posterior edge. The first member of the pair passes back from the rostralo-premaxillary with its ventral edge in contact with the maxilla. Posteriorly it abuts the suborbital and the other infraorbital. The second infraorbital passes upwards articulating with the anterior edges of the two suborbitals. Dorsally it adjoins a small fragment of bone (see 38123) which represents part of the dermosphenotic. The infraorbital sensory canal can be traced from the dermopterotic, into the dermosphenotic, where it turns sharply downwards and passes round through the infraorbitals into the rostralo-premaxillary. The two suborbitals are largish bones which fit in between the infraorbitals and the concave anterior edge of the maxilla and preopercular. The maxilla and preopercular are typically Palaeoniscid in structure. The maxilla is much broadened posteriorly and is long and slender anteriorly. The oral border of the maxilla bears teeth along its entire length, the teeth being in two series, an outermost series of small, numerous, sharply pointed teeth, and an inner series of much larger, less numerous and slightly curved teeth. The preopercular sensory canal runs along the posterior border of the preopercular, and the supramaxillary canal is represented by a distinct groove which passes from the antero-dorsal region of the preopercular down into the maxilla (*hc.* in Text-fig. 5).

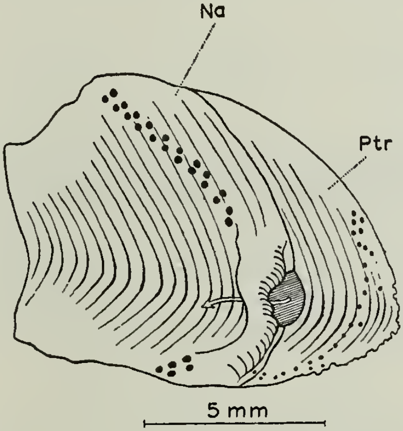

FIG. 6. *Centrolepis aspera* Egerton. Nasal and postrostral bones of the left side showing internal nares. From B.M.N.H. P 5594.

From the angle of the opercular bones the suspensorium is very oblique, with the opercular lying almost horizontal above the preopercular. The opercular is almost twice as long as it is broad and is a little larger than the subopercular. The subopercular is more vertical in position and as broad as it is deep. The number of branchiostegal rays that can be counted with any accuracy is twelve, although this is probably a little less than the correct number.

Lower jaw. The bones of the lower jaw are well preserved in P 5594 (Text-fig. 7). The greater portion of the jaw is made up of the dentary. The surangular is small and forms a neat socket for the articulatory surface of the upper jaw. The remainder of the posterior edge of the jaw is made up of the angular. This bone does not seem to pass very far forwards, but since the inner surface of the jaw is not exposed its true extent cannot be determined. The dentary overlaps the angular and the surangular. Dorsally the dentary has a series of teeth on it. These teeth are of two sizes, much as in the maxilla, the outermost series being more closely set, of medium height, thin and sharply pointed (t_1), whilst labial to these is a series of much larger widely spaced teeth (t_2). Both sets of teeth are on the edge of a shelf which is formed by a continuous coronoid. The coronoid on its lingual surface bears a series of large tubercles (t_3), much larger than the shagreen of small rounded denticles on the palate and branchial apparatus.

Palate. The structure of the palate of *Centrolepis* is shown on the same specimen P 5594 (Text-fig. 8). Here practically the whole of the palate is visible with the exception of the posterior end, which is somewhat obscured by the hyomandibular and parts of the branchial apparatus. The suprapterygoid series is represented by one bone only, which runs the whole length of the dorsal border of the palate. This single suprapterygoid is expanded posteriorly where it joins the metapterygoid and pterygoid, but becomes much reduced as it continues forwards. Anteriorly the suprapterygoid broadens again slightly. Posteriorly beneath the suprapterygoid and between it and the ectopterygoid, is a small metapterygoid. The suture line between the metapterygoid and the pterygoid is rather indistinct, but by examination under xylol and carbon tetrachloride it could be discerned. The ectopterygoid, which forms the postero-ventral portion of the palate, bears a single row of large tubercular teeth on its lateral margin, and this row is continued forward on to the palatine. The rest of the palate is made up of the large pterygoid which passes forward and ends rather bluntly. The pterygoid extends from the ethmoid region backwards to terminate some distance in advance of the quadrate, between the metapterygoid

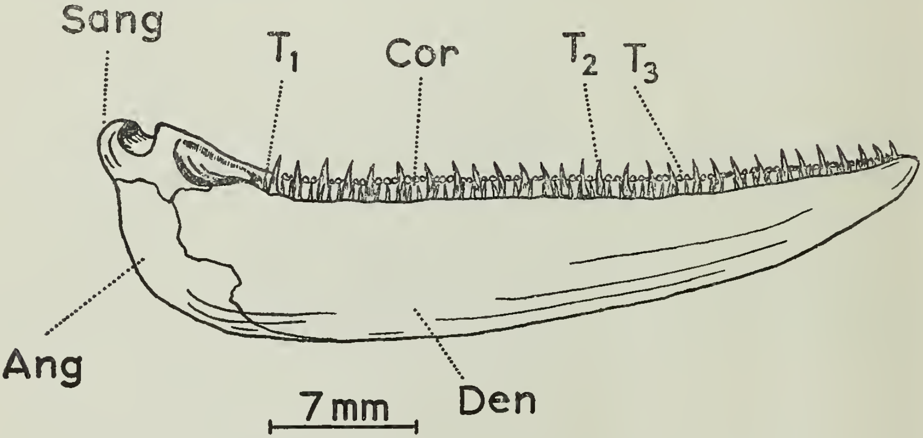

FIG. 7. *Centrolepis aspera* Egerton. Lower jaw, from B.M.N.H. P 5594, dentition from B.M.N.H. P 38123.

and the ectopterygoid. The palatine is represented by a narrow strip of bone lying between the lower border of the pterygoid and the maxilla.

Hyobranchial apparatus. This too can be seen in specimen P 5594 where it has been a little distorted and crushed during fossilization (Text-fig. 9). The hyomandibular is represented by a thin rod of bone somewhat expanded dorsally to become blade-shaped. It overlies the upper border of the suprapterygoid, but its connection with the quadrate cannot be seen. No trace of the ceratohyals can be found, although both hypohyals are present. The hypohyal is a stout ossification, with a V-shaped posterior border. This is articulated with a conical almost pointed basihyal. Behind the basihyal are two median basibranchials similar to those described by Watson (1925 : 863) for *Elonichthys aitkeni*. The first and second branchial arches have long hypobranchials, those of the third and fourth being slightly shorter. The four ceratobranchials are slender and the first two are only partly preserved in this specimen. The fourth ceratobranchial is the most complete and has a small protuberance facing posteriorly near its dorsal extremity. The basihyals, hypohyals and basibranchials are all covered with a shagreen of fine denticles and traces of this also appear on the hypobranchials. It is probable that the whole branchial apparatus was covered with such denticles.

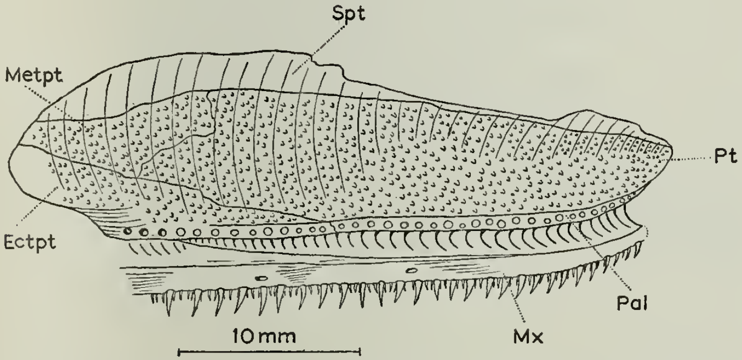

Fig. 8. *Centrolepis aspera* Egerton. Left side of palate viewed from its admesial surface, mainly from B.M.N.H. P 5594.

Appendicular skeleton. The supracleithrum is very long and extends down from the suprascapular to well beyond the junction of the opercular and subopercular (Text-fig. 5). It is ornamented with coarse tubercles similar to the patterning found on the skull roofing bones. The postcleithrum is also long—about half the length of the supracleithrum—with similar ornamentation, except near its posterior edge where the tubercles fuse into striae.

The cleithrum is both deep and robust, heavily ornamented with tubercles and ridges, especially posteriorly (Text-fig. 10). The antero-dorsal margin is distinctly concave and helps to form the posterior boundary of the gill chamber. The convexity in its lower posterior margin on the other hand is less pronounced. The clavicle is another stout ossification and posteriorly overlaps the end of the cleithrum (in P 5594 it has been displaced). In profile the clavicle is approximately triangular, and has a well-marked foramen (*f*) running through it. In describing the pectoral girdle of the Palaeoniscoid *Acrorhabdus bertili*, Stensiö (1921 : 229) figures a nerve canal running through the primary girdle plate. Since this foramen in the clavicle of *Centrolepis* would be in a direct line with such a nerve canal I think it more reasonable to suppose it transmitted nerves rather than blood vessels.

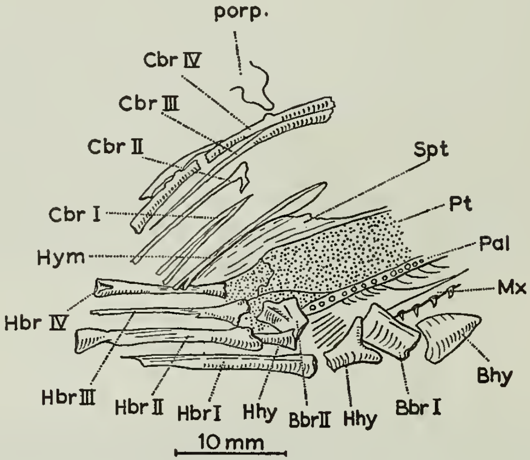

FIG. 9. *Centrolepis aspera* Egerton. Hyobranchial apparatus, left side. From B.M.N.H. P 5594.

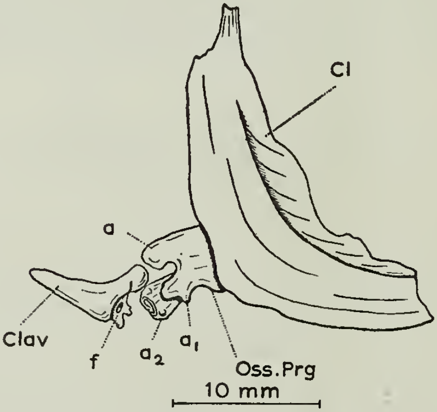

FIG. 10. *Centrolepis aspera* Egerton. Cleithrum, clavicle and primary girdle, from B.M.N.H. P 5594.

A primary girdle plate is present in this specimen and projects from beneath the postero-ventral margin of the cleithrum (Text-fig. 10). The outermost portion is a thin plate produced into two blunt processes (*a* and a_1) which face posteriorly. Beneath it and a little deeper is a stouter portion pointing backwards and downwards (a_2). No radials or lepidotrichia are visible.

The structure of the pectoral fin on 38123 shows it to possess between twenty-five and thirty stout lepidotrichia. The pelvic fin has between thirty and thirty-five and the anal much fewer, between fifteen and twenty.

Unpaired fins. The dorsal fin is quite long-based, with thirty to thirty-five lepidotrichia. The dorsal and anal fins are triangular in shape, the dorsal opposed to the space between the pelvic fins and the anal. Nothing further of the axial skeleton can be made out on any of the other specimens.

Squamation. The scales are thick, of moderate size and highly ornamented. In the abdominal region the scales have ridges and denticles which run along their length, but in the anterior region of the scale the ridges run vertically. In the caudal area the scales are coarsely serrated posteriorly, with a few short ridges anteriorly.

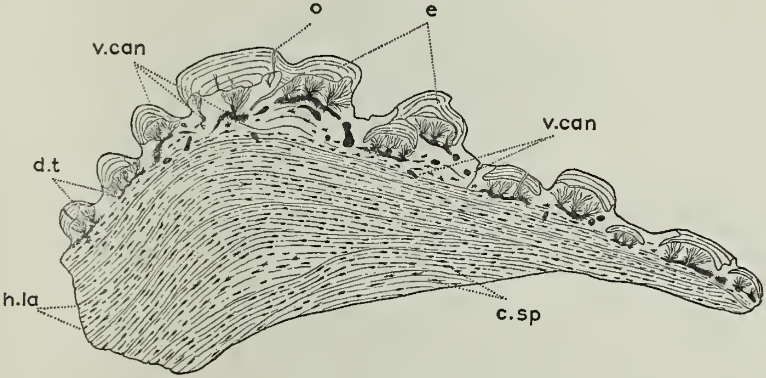

FIG. 11. *Centrolepis aspera* Egerton. Oblique section of scale, B.M.N.H. 11260, much enlarged.

From a microscopic examination the scales are obviously similar to the " Palaeoniscoid " scale of Goodrich (1907) and agree closely with the structure of scales of other Palaeonisciformes described by Ørvig (1957).

The scales (Text-figs. 11, 12) are made up of a superficial layer of enamel (*e*) and dentine, with a basal portion of laminar bone (*h. la.*). Beneath the enamel, which is often raised up into ridges and tuberculations, is a horizontal network of canals (*v.can.*). Occasionally from this network a vertical canal arises and pierces the surface of the enamel (*o*). Also from this horizontal network arises a system of long upwardly directed dentinal tubules (*d.t.*). Beneath the horizontal canal system the laminar bone occurs, showing the primitive condition where the bone tissue contains cell spaces throughout its length (Text-fig. 11). These cell spaces (*c.sp.*) are more or less horizontally arranged and follow the course of bone lamellae. This basal bone is penetrated by numerous thin vascular canals of Williamson (*can.W.*). These canals run somewhat obliquely upwards from the basal portion of the scale. The canals are thin and of characteristic shape much as in *Orvikuina* (Ørvig, 1957, fig. 3), possessing short ramified side twigs (*s.br.*). Unlike *Orvikuina* they do not contain the cells which gave rise to the bone lamellae, instead these cells are arranged between the canals of Williamson. Their distribution here is random, and there is no concentration around the canals.

In general perspective the scale of *Centrolepis* appears primitive and shows little specialization, the canals of Williamson still appearing to retain their vascular function, the bone cells being randomly arranged, the dentine layer is still present, and the whole scale is capped with a layer of enamel.

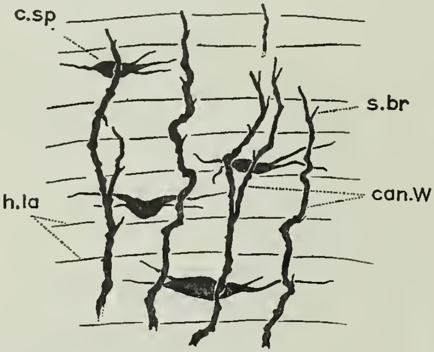

FIG. 12. *Centrolepis aspera* Egerton. Vertical section of the basal bone tissue of the scale. ×250 approx. B.M.N.H. 11260.

" *SUBHOLOSTEI* "

Family PLATYSIAGIDAE

DIAGNOSIS. Subholostean fishes of elongate-fusiform shape with deeply forked equilobate tails. Paired fins Holostean in structure and of moderate size. Fins have numerous small fulcra, the lepidotrichia are stout and bifurcated and all articulated distally. The mandible has a broad coronoid process, the dentition consists of a series of large, conical, pointed teeth, interspersed with numerous, irregularly arranged smaller teeth. The maxilla is Palaeoniscid in make-up, but the preopercular is much expanded and the suspensorium upright. Branchiostegal rays well developed. External skull bones heavily ornamented, with tubercles and ridges. Scales thin, rhombic, covered with enamel and ornamented with feeble ridges and a few scattered tubercles anteriorly. The posterior margins of the scales are denticulated.

Genus ***PLATYSIAGUM*** Egerton, 1872

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. *Platysiagum sclerocephalum* Egerton.

REMARKS. The genus contains two species, *Platysiagum sclerocephalum* Egerton from the Lower Lias of Lyme Regis, and *Platysiagum minus* Brough from the Middle Trias of Besano.

The genus was first described by Egerton (1872 : no. 6, pl. 6) as belonging to the order Ganoidei and to the heterogeneous family the Sauroidei. Later Woodward (1895*b* : 532) included it in the Palaeoniscidae. He was of the opinion that the arrangement of the cheek plates alone was sufficient for determining the systematic position of the genus.

It was not until 1939 that Brough (p. 18) recognized the genus as being more Holostean in affinities than Palaeoniscoid. His conclusions were substantiated by the discovery of the second species, *Platysiagum minus*, in the fauna collected from Besano. This species had somewhat better preserved fins than are found in any of the existing specimens of *Platysiagum sclerocephalum*, and from the nature of the paired fins (which are distinctly Holostean), the hemiheterocercal tail and the incipient interopercular, Brough concluded that the genus was at the Subholostean level of evolution.

Platysiagum sclerocephalum Egerton

(Text–fig. 13)

1872. *Platysiagum sclerocephalum* Egerton, no. 6, pl. 6.
1895*b*. *Platysiagum sclerocephalum* Egerton : Woodward, p. 533.
1939. *Platysiagum sclerocephalum* Egerton : Brough, p. 17.

DIAGNOSIS. A *Platysiagum* comprising fishes of moderate to large size. Length of head much exceeding the maximum depth of the trunk. Tuberculations on scales sparse.

SYNTYPES. B.M.N.H. P 3650, P 1333 and P 558, from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H. and the Geological Survey Museum.

DESCRIPTION. *The skull.* In shape the head must have been quite blunt, and rounded anteriorly (Text-fig. 13). The external bones of the skull are stout and presumably articulated closely with one another. The ornamentation varies in character according to the position of the bone. Thus the bones constituting the top of the head are heavily ornamented with series of tubercles and ridges, which are especially prominent on the frontals. On the cheek bones the ridges are less frequent and the ornamentation generally less coarse. The opercular bones have only a slight ornamentation of small tubercles anteriorly, with an almost smooth posterior portion. Contrary to Woodward's statement (1895*b* : 533), the branchiostegal rays and gular plate are well ornamented. On a specimen in the Geological Survey Museum (G.S. 94743) the former can be seen to be ornamented with a fine, almost regular series of smaller tubercles. The pattern of ornamentation of the lower jaw is more coarse, very similar to that found on the frontals.

Very little can be made out of the bones of the skull roof. The major portion seems to have been formed by the frontals, but the extent of the other roofing bones is not clear. Posteriorly there appears to be a demarcation into suprascapulars and extrascapulars, but the limits of these cannot be defined with certainty. Passing forwards and downwards, the frontals abut on to the postrostral bone. Anterior to the postrostral is another bone, well shown in B.M.N.H. P 3650, occupying a medial position. This is the rostral bone, and it has a markedly rounded outline. The ornamentation of the rostral is rather remarkable, as it has a series of ridges running round it almost in half circles, reminiscent of the peculiar spiral ridges found on the postrostral of *Ptycholepis curta*.

The postrostral articulates laterally with the nasals, and with the rostral anteriorly. The premaxilla is a small ossification seen in B.M.N.H. P 3650, where it has three or four large teeth. The antorbital is a fairly large bone whose structure can be made out from B.M.N.H. P 3651. Antero-dorsally the antorbital articulates with the rostral bone, and in this region it is cut into by a pronounced semicircular notch, which can only be the nasal orifice. Ventrally part of one side of the antorbital abuts the maxilla, whilst more dorsally it articulates with the infraorbital. Anteriorly it joins the premaxilla. The dorso-posterior edge of the antorbital borders a small portion of the orbit. Posterior again to the antorbital and limiting the orbit behind and below is a series of two infraorbitals and a dermosphenotic. The first infraorbital is a slightly curved bone which broadens a little anteriorly to articulate with the

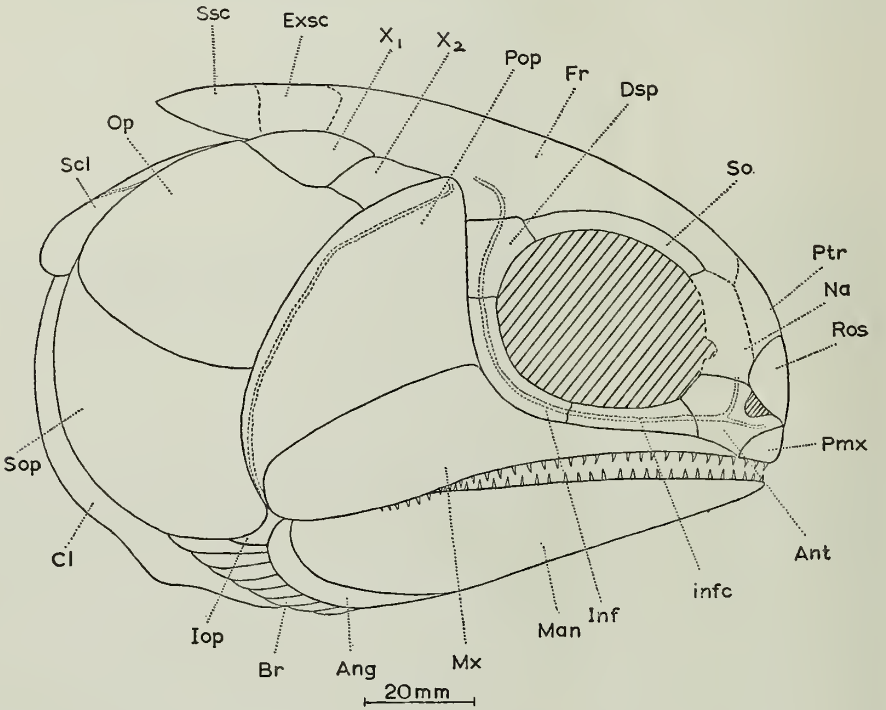

FIG. 13. *Platysiagum sclerocephalum* Egerton. Reconstruction of the right side of the head.

antorbital. Posteriorly it joins the second infraorbital which runs along part of the maxilla anteriorly, but passes backwards and upwards to border part of the preopercular as well. Above the infraorbital is a shorter stouter bone, the dermosphenotic. Dorsally the orbit is limited by a supraorbital bone, of much the same dimensions as the infraorbitals. Possibly this bone may have been made up of more than one element, but I was unable to ascertain this because of the poor state of preservation of the specimen.

The course of the sensory canals can be traced in places. The infraorbital canal is just visible in the dermopterotic, from where it runs through the dermosphenotic and on round the two infraorbitals into the antorbital. In the latter bone it branches into two, each branch passing to either side of the nasal orifice. The preopercular canal can be seen running through the postero-dorsal edge of the preopercular.

The major portion of the cheek is covered by two bones, the preopercular and the maxilla. The cheek region is characteristically of Palaeoniscoid form, apart from the very enlarged preopercular. The latter bone is a very large element, whose posterior edge describes a sweeping curve. This posterior margin is nothing like the straight edge found in *Platysiagum minus*. Along its entire length, the lower border of the preopercular is in very close contact with the maxilla. The maxilla is essentially Palaeoniscoid in pattern, with an enlarged rectangular posterior portion. Anteriorly it sweeps downwards and forwards, tapering almost to a point. Along its entire ventral length the maxilla bears teeth. The dentition consists of a series of large conical, sharply pointed teeth, interspersed with numerous irregularly arranged teeth.

The opercular cover consists of two principal plates of semicircular shape, the opercular and subopercular. The two plates are of approximately the same size, with rounded posterior margins. The effect is a continuous curved outline which runs down uninterrupted from the suprascapular to the first branchiostegal rays. Along the dorsal margin of the opercular lie two smaller bones, probably corresponding to Traquair's bone " X " (1901 : 83). They are members of the opercular series and not the preopercular series, since the preopercular sensory canal passes along the posterior border of the preopercular in such a position as would make it impossible for it to pass through either of the two bones. The more anterior of the pair, X_2, adjoins the preopercular. The interopercular is a small ossification, filling the gap between the end of the subopercular and the lower jaw.

There are eighteen to twenty branchiostegal rays on each side, and these are quite thin posteriorly, but increase in width anteriorly. The lower jaws are stout and bear numerous teeth along their posterior margins. The teeth are confined to a broad platform, and are similar to those found on the maxillae. Posteriorly this margin expands upwards into a large coronoid process. The bones of the lower jaw cannot be identified, but on B.M.N.H. P 558 the extent of the angular can be made out. This bone forms the most posterior margin of the jaw, but occupies only a small portion of its length. In front of the branchiostegal rays and between the jaw rami, a large ornamented gular plate is shown in G.S. 94743.

Of the other skull bones little remains. However, in specimen B.M.N.H. P 2046, the parasphenoid, pterygoid and ectopterygoid can be distinguished. The parasphenoid has a central area devoid of teeth, but on either side of this is a tooth series. In this series there are again two types of teeth, the larger, sharply pointed ones, and the smaller irregular teeth between them. The teeth are somewhat smaller than those found on the maxillae and mandibles. Alongside the parasphenoid are bits of the ectopterygoid and pterygoid ; these are covered by very fine granulations, or minute teeth.

Appendicular skeleton. The supracleithrum is a long bone much expanded ventrally, so that it is spatulate in shape. The ornamentation consists more of sculpturing than of tuberculations, giving it a pitted effect. The cleithrum is a relatively stout ossification with a distinct depression in it posteriorly for the reception of the pectoral fin. The ornamentation in this case is much more rugose with ridges rather than tubercles. The cleithrum is much broadened, and thicker ventrally. The pectoral fin consists of about twenty rays, with the anterior rays unjointed along most of their length. The first two rays anteriorly have a fringe of spiculae, but this is absent on the remainder. The fin insertion is constricted and narrow.

The pelvic fins have about twelve fin rays and again have a markedly constricted insertion. The general shape and structure of the paired fins is of distinctly Holostean form.

Unpaired fins. The dorsal fin consists of only a few stout rays, between ten and fifteen, but no evidence of an anal fin could be found on any of the specimens. Brough (1939 : 18) states that in *Platysiagum sclerocephalum* " the dorsal fin consists of about fourteen such rays ; those of the anal cannot be counted accurately ". Whatever he was looking at was certainly not an anal fin, since Woodward (1895*b* : 533) also failed to find any evidence of this fin.

The true structure of the caudal region is impossible to determine, but from Brough's (1939 : 17) notes on the species, and from his discovery in *Platysiagum minus* of a complete tail, it is probably correct to say that the tail in *Platysiagum sclerocephalum* was not completely heterocercal, but nearer the Holostean condition.

REMARKS. The genus *Platysiagum* is obviously of Palaeoniscoid origin. The characteristic maxilla still firmly united to a large preopercular as the essential cheek covering is most certainly a relic of its Palaeoniscoid ancestry. Higher members of the " Ganoid " grade have smaller, freed maxillae, and very much reduced preoperculae. However, the interopercular bone so characteristic of the Holostei is present in *Platysiagum sclerocephalum*, but a large opercular and subopercular still cover the gill chamber. The orbit is large and placed anteriorly, and has a complete set of infraorbital bones. In fact, the skull has departed little from the arrangement found in the Palaeoniscoidea.

The more advanced characters of the skull seem confined to the lower jaw where a coronoid process has developed and is overlapped by the posterior extremity of the maxilla. *Platysiagum* resembles the Semionotidae in its fusiform body and in the structure and distribution of its fins. This, together with the hemiheterocercal tail, the interopercular and the rhombic, ganoid scales, shows it to have progressed from the typical Palaeoniscoid make-up towards that found in the Holostei. This isolated genus was just another offshoot from the Palaeoniscoids, which had a short existence and eventually came to nothing.

Family PTYCHOLEPIDAE

DIAGNOSIS. Subholostean fishes, ranging from small to large size. Trunk elegantly fusiform and snout acutely pointed. Caudal fin deeply forked and hemi-heterocercal. Suspensorium almost vertical, gape wide and orbit large. Dentition consisting of two series of small close-set teeth. Ornamentation of skull roofing bones distinct, with high ridges of enamel running more or less longitudinally.

The frontals are large and elongated, and constitute the major portion of the skull roof. The parietals are rectangular and much smaller. The elongated dermosphenotics border the frontals laterally, separating them from the orbit. The jaws are long, and the maxillae slender anteriorly. The maxilla is surmounted by a small triangular infraorbital.

The snout is covered by a large postrostral, bordered on either side by a pair of nasals. The opercular apparatus is somewhat quadrangular in shape, the opercular much deeper than wide and considerably larger than the subopercular. The first branchiostegal ray is much enlarged and there is a big gular plate in all species. There is no interopercular, and the pectoral girdle has a stout clavicle present.

The squamation is dense, scales thick, longer than wide and much elongated in the ventral region. The pectoral and pelvic fins well developed, dorsal and anal fins triangular, the former opposed to the pelvics, the latter small and remote. Fulcra conspicuous on all fins, biserial.

REMARKS. This family was originally associated with the Furidae (Woodward, 1895*b*: 316), but Brough (1939 : 17) and Aldinger (1937 : 276) have shown its affinities to be more with the Palaeoniscids and have traced its ancestry back to the Palaeoniscid *Boreosomus*.

Genus ***PTYCHOLEPIS*** Agassiz, 1833

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. *Ptycholepis bollensis* Agassiz.

Ptycholepis monilifer Woodward

(Plates 36–40)

1895*b*. *Ptycholepis monilifer* Woodward, p. 322, pl. 10, figs. 2–4.

DIAGNOSIS. A *Ptycholepis* of large size, not less than 60 cm. in length. Ornamentation fine. Lepidotrichia ornamented with oblique ridges of enamel. Scales long and slender, with a few tubercles anteriorly, passing into long ridges which run downwards and backwards occasionally anastomosing.

HOLOTYPE. Fish in four pieces, B.M.N.H. 39868, from the Lower Lias, Lyme Regis.

REMARKS. The sole specimen of this species is 39868, from the Lower Lias of Lyme Regis. It is in four pieces, but, since these were collected at the same time and by a reliable collector, there is no reason to doubt that all four belong to one and the same specimen.

The only description is that given by Woodward (1895*b* : 322). A re-examination of this material has shown that Woodward has misinterpreted some of the bones, and since he figured only the lower jaw and a few scales, I am redescribing the species.

DESCRIPTION. On the first block (Pl. 36) there is a stout right mandibular ramus, very similar in shape and make-up to *Ptycholepis bollensis*. The jaw is 9·75 cm. in total length with a depth of approximately 2·4 cm. The alveolar border has a marked sigmoidal curvature, the highest point being 1 cm. anterior to the articulatory facet. There is a single series of small, robust, conical teeth. These teeth are markedly striated longitudinally around their bases, but have an almost smooth cap, reminiscent of the condition found in the Saurichthyids. The anterior extremity of the jaw tapers to a blunt point, where the ornamentation is coarser than over the remaining jaw surface. The ornamentation generally consists of superficial ridges, which although very irregular, pass upwards and forwards from the ventral margin. The ridges branch and interdigitate, but are nowhere near as coarse as those found on the lower jaw of *Ptycholepis bollensis*. Dorsally near the alveolar margin the ornamentation breaks up into isolated tubercles.

The surangular, a small bone bordering the articular facet, forms the most posterior portion of the jaw. The remainder of the posterior edge of the jaw is composed of the angular, which passes forwards and downwards from the anterior end of the articular facet. This bone also forms part of the lower border of the jaw, extending along almost half of its length. The bulk of the mandible is composed of the dentary, along which the course of the sensory canal is clearly marked by a series of pits. This mandibular canal finishes 5 mm. short of the anterior extremity of the jaw. Posteriorly the sensory canal can be traced back on to the angular, but its passage back up through the surangular is a little obscure. Lying above the jaw on the same block is a ceratohyal. It is fragmented anteriorly but the outline still remains on the underlying matrix. Posteriorly the bone ends bluntly, but passing forwards it narrows, and then broadens into an almost spatulate shape. Since this is the largest species of *Ptycholepis* the length of the ceratohyal can usefully be given as 5·45 cm.

On the second block (Pl. 37), the principal bone is the large right maxilla, incorrectly called a suboperculum by Woodward (1895*b* : 322). After a little development with needles, a set of teeth became apparent along its lower, somewhat concave border. These teeth are very similar in shape, size and pattern to those on the dentary. Occasionally the smooth cap has a semblance of striae on it. The maxilla is much longer than deep, over three times as long as its maximum depth. Its total length is 6·1 cm. after reconstruction, the outline of the posterior end, which is missing, being again easily seen on the underlying matrix. Dorsally it is overlain by the large first branchiostegal ray, but from the posterior extremity the maxilla sweeps forwards and upwards, then flattens out, and finally anteriorly it curves down again to form a short anterior process which bordered the lower rim of the orbit. Part of the anterior end of the maxilla has been broken off and is missing. Antero-dorsally the edge of the maxilla forms a narrow unornamented shelf, and on to this probably fitted an infraorbital series of bones. Elsewhere the maxilla is highly ornamented with ridges of enamel. These ridges follow the length of the bone, but posteriorly sweep round almost in contour fashion ; those in the dorsal region sweeping upwards, forming whorls of ridges, those in the ventral region sweeping downwards.

The bone on top of the maxilla, which Woodward (1895*b* : 322) called a large gular, is in fact this first enlarged branchiostegal ray. Then again, the bone which overlies the anterior extremity of the first branchiostegal ray is probably a member of the postorbital series. Both these last bones are practically smooth, but with the first branchiostegal ray having a small mesial area with a few isolated tubercles on it. On the same block there are ten other branchiostegal rays, very much narrower than the first, and all delicately ornamented with ridges and tubercles of enamel. Lying beneath the maxilla is a stout ossification, the homology of which it is almost impossible to decide. Rather tentatively I suggest that it is the crushed primary girdle element. Lying to the side of this is another indeterminate bone, which could be a clavicle.

The third block (Pl. 38) is much larger and contains the dorsal fin. The dorsal fin consists of about thirty lepidotrichia, with a few small slender rays anteriorly ; these increase in length up to the seventh or eighth ray, and then progressively shorten as the fin passes backwards. No fulcra could be observed and the rays are undivided. All the rays were ornamented, especially near their bases. Anteriorly the ridges of enamel run diagonally across the stouter rays, but posteriorly the ridges run more parallel to the length of the rays.

Three of the body scales from this block have already been figured by Woodward (1895*b*, pl. 10, fig. 3). The scales are long and slender, with a few tubercles anteriorly passing into long ridges of enamel which run obliquely downwards and backwards (Pl. 40). These ridges sometimes branch and intercalate, but normally all terminate on the ventral border of the scale. The scales exhibit a delicate peg-and-socket articulation, not as strong as in *Lepidotes*, but again not really feeble as Woodward (1895*b* : 323) suggests. The peg is antero-dorsal in position being much nearer the anterior extremity, about a quarter of the way along its dorsal length. Also on this block is another large bone, with an ornamentation similar to that found on the maxilla. It is 6·5 cm. in length with its anterior margin produced into a sharp spur. The only bone with which it corresponds is the preopercular described in *Ptycholepis barboi* by Brough (1939, fig. 27). It is broader dorsally, with a distinct cleft, presumably for articulation with the dermopterotic. The posterior border is convex, whilst much of the outer surface of the bone is ornamented. The ornamentation is mainly in the form of ridges of enamel which sweep inwards from the posterior margin towards the spur. Dorsally there are a few tubercles and on either side of the spur the ridges form two whorls. Around the antero-dorsal cleft the bone is devoid of ornamentation, and again the spur and anterior edge of the bone are smooth. Running down the length of the bone is a distinct groove, this probably marks the course of the preopercular sensory canal, since in the dorsal region several distinct pits are visible.

Finally, the fourth block (Pl. 39) contains the caudal fin. This fin is large, 21 cm. from tip to tip, deeply cleft and strongly heterocercal. The lower lobe is somewhat the larger of the two, although the upper lobe was obviously produced, as is usual in this genus. The lepidotrichia are very numerous, stout anteriorly, but becoming very delicate and dichotomizing in their distal parts. The joints are stout proximally, but distally they are always longer than broad and often somewhat attenuated at the middle. The dorsal lobe has a double row of strong ridge scales along its dorsal edge. These scales are well developed and ornamented with tubercles and ridges of enamel.

Ptycholepis bollensis Agassiz

(Text-figs. 14–18)

1832. *Ptycholepis bollensis* Agassiz, p. 142 (name only).
1833. *Ptycholepis bollensis* Agassiz, **2**, pt. 1, p. 11.
1835. *Ptycholepis bollensis* Agassiz : Agassiz, **2**, pt. 2, p. 108, pl. 58*b*.
1849. *Ptycholepis bollensis* Agassiz : Williamson, p. 444.
1852. *Ptycholepis bollensis* Agassiz : Quenstedt, p. 203, pl. 15, fig. 5.
1856–58. *Ptycholepis bollensis* Agassiz : Quenstedt, pl. 30, figs. 1–7 ; pl. 31, fig. 8.
1865. *Ptycholepis bollensis* Agassiz : Cotteau, p. 337.
1875. *Ptycholepis bollensis* Agassiz : Sauvage, p. 8, pl. 2, fig. 2.
1891. *Ptycholepis bollensis* Agassiz : Sauvage, p. 33, pl. 1.
1895*b*. *Ptycholepis bollensis* Agassiz : Woodward, p. 317.
1896. *Ptycholepis bollensis* Agassiz : Woodward, p. 36, pl. 5.
1896. *Ptycholepis bollensis* Agassiz : Scupin, p. 169, pl. 10. fig. 5.
1919. *Ptycholepis bollensis* Agassiz : Hennig, p. 173.
1935. *Ptycholepis bollensis* Agassiz : Gross, pl. 7, fig. 2 ; text-figs. 27–29.
1937. *Ptycholepis bollensis* Agassiz : Aldinger, p. 286, text-figs. 85, 86*a*, 87*b*, 88*b*.
1952. *Ptycholepis bollensis* Agassiz : Hauff, p. 23, pls. 42, 43.

DIAGNOSIS. A *Ptycholepis* of moderate size, attaining a length of some 35 cm. Body fusiform, deepened anteriorly. Orbit large, length of the head about a quarter of the total length of the fish and equals the maximum depth of the trunk.

HOLOTYPE. A much crushed and distorted fish, B.M.N.H. P 3688, from the Upper Lias of Whitby, Yorkshire.

MATERIAL. Specimens in the B.M.N.H., the Royal Scottish Museum, Edinburgh and the Tübingen Museum.

REMARKS. This species was described by Agassiz (1835 : 108) and it is confined to the Upper Lias. Specimens come from the Upper Lias of Yorkshire, Germany and France.

DESCRIPTION. *The skull.* All the skull roofing bones are ornamented and patterned by deep grooves and ridges of enamel. These ridges are very coarse on the parietals, frontals, dermopterotics, suprascapulars, and dermosphenotics, where they run longitudinally along the length of the bones. The ridges run more obliquely on the extrascapular, and on the nasals they follow the sweep of the bone. Only the posterior half of the postrostral is ornamented by these parallel, longitudinal ridges ; the anterior half is completely smooth with its forward edge characteristically scalloped. The postorbital bones and the infraorbital show finer longitudinal ridges, but on the maxillae these ridges become broken up anteriorly into tubercles. The ornamentation of the opercular is more diffuse with ridges of enamel running more or less downwards in gentle curves from the antero-dorsal region (Text-fig. 14). The subopercular again shows longitudinal ridges, whilst the ornamentation on the mandible can be seen from Text-fig. 15. The first branchiostegal ray has a slight indication of ridging anteriorly, but the remaining rays and the median gular are comparatively smooth.

The character of the ornamentation of the skull roof makes the interpretation of the suture lines in that region difficult. However, one specimen of *Ptycholepis bollensis*, No. 10800, from the Upper Lias of Ohmden, Württemberg, in the Tübingen Museum, is flattened dorso-ventrally and shows the whole skull roof. From this specimen it was possible not only to work out the demarcation of the individual bones, but to trace the branches of the sensory canal system.

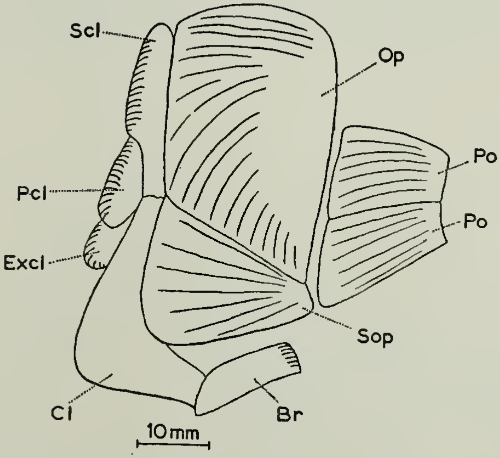

FIG. 14. *Ptycholepis bollensis* Agassiz. Sketch of a specimen from the Lias of Holzmaden, Germany, in the Tübingen Museum.

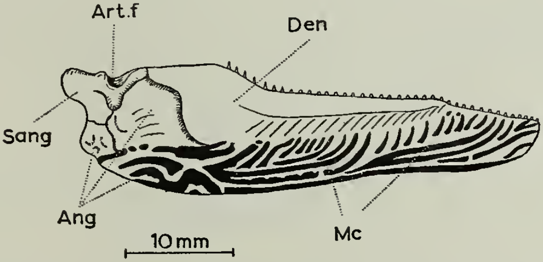

FIG. 15. *Ptycholepis bollensis* Agassiz. Lower jaw from B.M.N.H. P 3691*a*, dentition restored.

The major portion of the skull roof is made up of the large frontals (Text-figs. 16, 17). These are fairly narrow bones, broadened slightly near their centre. The suture between them is straight and does not interdigitate. Anteriorly the frontals end quite bluntly where they abut on to the postrostrals, and do not have the V-shaped insertion between the postrostral and nasals described by Brough (1939 : 68) in

Ptycholepis curta. Anteriorly the frontals border a small portion of the orbit. The parietals are about a third of the length of the frontals and are squarish in outline. Behind the parietals is a pair of extrascapulars. These, however, do not meet in the mid-line. Posteriorly to the extrascapulars, and a little below them, are the small suprascapulars.

Bordering the suprascapular and extrascapular anteriorly is a very large bone, the dermopterotic. This bone also borders the complete lateral edge of the parietal and part of the postero-lateral edge of the frontal. Abutting on the dermopterotic anteriorly and extending forwards is a long narrow ossification, the dermosphenotic.

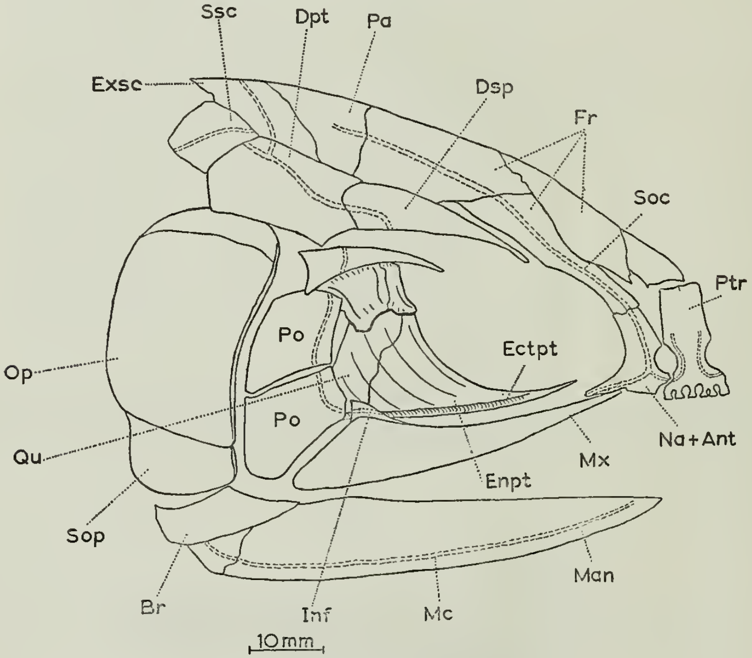

FIG. 16. *Ptycholepis bollensis* Agassiz. Sketch of a specimen from the Lias of Holzmaden, Germany, in the Tübingen Museum.

The dermosphenotic is broadened somewhat posteriorly, where it meets the dermopterotic, but narrows as it passes forwards. It borders the frontal laterally along most of its length, and forms part of the dorsal rim of the orbit. It does not, however, reach the nasal as in *Ptycholepis curta.*

The majority of the remaining description is based on a specimen (unnumbered) in the Tübingen Museum, from the Lias of Holzmaden, catalogued under the Keppler collection. The structure of the snout is typically Palaeoniscid, composed mainly of a prominent postrostral element. This bone passes from the frontal forwards and downwards and is then tucked back under to form part of the ventral surface. Posteriorly it is relatively narrow and its lateral edges parallel, but anteriorly it broadens considerably as it passes round the snout. Laterally it is indented to form the anterior rim of the nasal orifice. On either side of the postrostral there is a large nasalo-antorbital bone. The nasalo-antorbital does not vary much in width and borders the entire lateral edge of the postrostral. Ventrally it is prolonged back under the orbit and has a neat recess into which the posterior extremity of the maxilla fits. Posteriorly the nasalo-antorbital borders the orbit, and anteriorly the nasal orifice. Along its ventral edge it bears a row of small teeth, suggesting that this bone I have termed nasalo-antorbital represents not just a fusion of the nasal and antorbital bones, but also includes the premaxillary element (see specimen No. 4628 from Boll, again in the Tübingen Museum, which shows the articulations of the maxilla, nasalo-antorbital and postrostral perfectly).

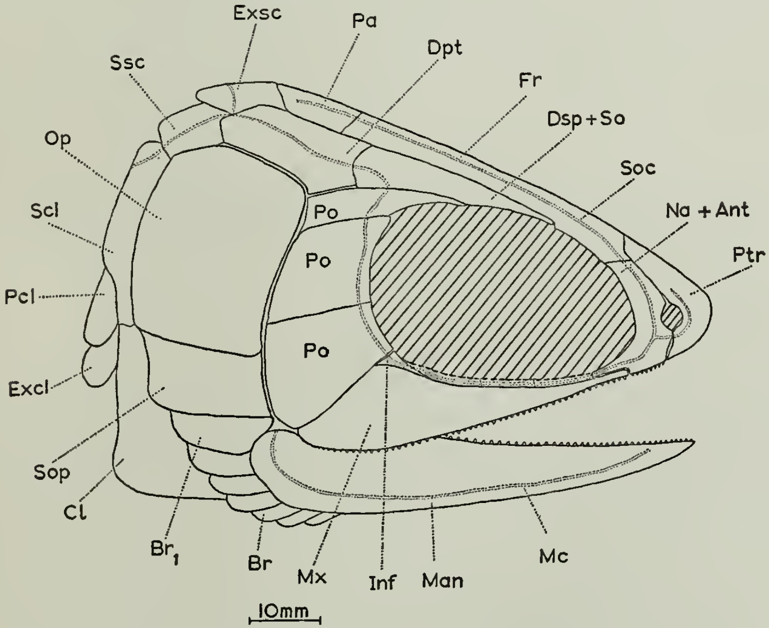

FIG. 17. *Ptycholepis bollensis* Agassiz. Restoration of skull and pectoral girdle.

The cheek region is characterized by the great development of the postorbital series of bones. This series completely covers the preopercular and excludes it altogether from the external surface of the skull. In the specimen of *Ptycholepis bollensis* from the Lias of Holzmaden, this series is completely preserved. There are three bones of which the first two are of roughly comparable size and shape, but the third, the most dorsal of the series, is much thinner and elongated. The first two border the orbit posteriorly, but the third forms part of the dorsal rim of the orbit, and fits neatly under the antero-ventral edge of the dermopterotic and the postero-ventral edge of the dermosphenotic. In shape it closely resembles the dermosphenotic but is much smaller. The edges of all three bones are distinct and there does not appear to be another series intervening between them and the orbit.

The maxilla and one infraorbital are well displayed on the same specimen. The maxilla extends from the first branchiostegal ray forward to where it meets the nasalo-antorbital. Posteriorly the maxilla is of triangular shape where it fits under the first postorbital, but as it passes forwards the maxilla tapers gently. The ventral border of the maxilla overlaps the mandible posteriorly, but in this region the border is not produced downwards so much as in earlier species.

The infraorbital is a small triangular bone firmly attached to both the upper border of the maxilla and to the antero-ventral corner of the first postorbital. The infraorbital sensory canal passes through this bone. The remaining bones of the infraorbital series, those which border the maxilla dorsally, are missing in the specimens examined. However, since the first one is present and the maxilla has a distinct ledge along its dorsal border, there is every reason to believe such a series was present.

The opercular bones together form a large quadrangular gill cover. The opercular is deeper than wide, approximately rectangular with a somewhat concave anterior border. The subopercular, although large, is much smaller than the opercular to which it is attached closely. It is much wider than deep and does not end in a sharp ventral angle as it does in *Ptycholepis curta*.

Immediately below the subopercular is the first branchiostegal ray. This ray is considerably enlarged and of distinctive shape, tapering to a point anteriorly. It appears to overlie the posterior extremity of the lower jaw. The remaining rays are smaller, about nine or ten in number, and the series ends with the median gular plate.

Lower jaw. The structure of the lower jaw could be well seen in a specimen of *Ptycholepis bollensis* from the Lias of Whitby (B.M.N.H. P 3691*a*) after mechanical preparation (Text-fig. 15). This specimen was figured by Woodward (1896, pl. 5, fig. 4), but the illustration shows nothing apart from the ornamentation. In the specimen the surangular bone forms the posterior dorsal corner of the mandible and has a deep recess for the articulation with the upper jaw. Below this articulatory facet the surangular is produced into a distinct ridge, and posteriorly behind the facet it forms a backward projection to the mandible. From this elbow-like projection the surangular runs down in a concave sweep to meet the angular. The angular is a much larger bone with little ornamentation dorsally, but with thick ridges of enamel running horizontally over its ventral region. Anteriorly the angular is thickened, making the junction with the dentary quite distinct. The remaining area of the admesial surface of the jaw is composed of the dentary. Ventrally the dentary has thickened ridges of enamel running more or less longitudinally, but nearer its superior border the ridges are turned upwards. The upper margin is not a straight line as in *Ptycholepis barboi*, but has a marked coronary prominence. The teeth are not shown in P 3691*a*, but on several specimens in the Tübingen Museum the dentition of the lower jaw is visible. There are two rows of small slightly rounded teeth running along most of the upper surface of the jaw.

Sensory canal system. The supraorbital canal commences well back in the parietal, and runs forward through the length of the frontal. Anteriorly it passes down into the nasalo-antorbital, where it joins the infraorbital canal.

The main cephalic division of the sensory canal crosses the antero-dorsal corner of the supracleithrum and passes forward through the dermopterotic. At its point of entry into the dermopterotic, it gives off the supratemporal commissure, which runs through the extrascapular. The main cephalic division then turns down through the posterior corner of the dermosphenotic as the infraorbital canal. The infraorbital canal passes round the anterior edge of the postorbitals, and down through the infraorbitals, finally entering the nasalo-antorbital. In the nasalo-antorbital it branches into two, the anterior branch passing into the postrostral where it ends blindly just above the nasal orifice. The posterior branch continues on through the nasalo-antorbital to fuse with the supraorbital canal. Most of the above account of the sensory canal system is based on specimen No. 8740 from Boll, in the Tübingen Museum.

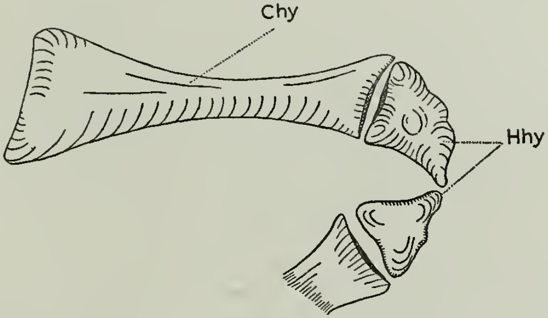

FIG. 18. *Ptycholepis bollensis* Agassiz. Ceratohyal and hypohyal. From a specimen from the Lias of Holzmaden, Germany, in the Tübingen Museum.

Palate. The palatoquadrate is very similar to that described by Stensiö (1921 : 211) for *Boreosomus arcticus*, and by Brough (1939 : 63) for *Ptycholepis barboi*. The palato-quadrate is a large ossification consisting of three principal elements, a quadrato-metapterygoid, an entopterygoid and an ectopterygoid (Text-fig. 16). In general shape the whole apparatus is triangular with its posterior margin almost vertical. The antero-dorsal margin is strongly concave and the ossification tapers almost to a point anteriorly. The most posterior bone is the quadrato-metapterygoid and is a large high bone. Dorsally it articulates with the orbitotemporal region of the neurocranium. The entopterygoid is also rather high and the distinct suture between it and the quadrato-metapterygoid is indicated in the sketch (Text-fig. 16). The entopterygoid forms most of the anterior portion of the palate. Beneath it is a narrow ectopterygoid running almost horizontally. This bone extends back to meet the quadrate. It is a much thickened ossification, and gives the edge of the palate a bevelled appearance. On the inner surface of the entopterygoid there is a distinct area bearing small tubercular teeth ; whether the quadrato-metapterygoid had a similar area could not be ascertained. The neurocranium must have been a stout ossification, because in one specimen in the Tübingen Museum (no number) the skull had been laterally crushed and the ossified neurocranium can be seen beneath the dermal bones. The most obvious portions are a distinct postorbital process and an ascending ramus of the parasphenoid.

Hyobranchial apparatus. Of the hyoid arch only the ceratohyal and the hypohyal can be seen (specimen No. 8739*c* in the Tübingen Museum). Both bones are stout with the ceratohyal cylindrical in cross-section (Text-fig. 18). The proximal ends of the ceratohyal are thickened, but the central region is a good deal thinner. The hypohyal is triangular in outline, well rounded and with a distinct facet for articulation with the ceratohyal.

Appendicular skeleton. The pectoral girdle is rarely seen and is invariably covered by the opercular bones. However, in yet another specimen in the Tübingen Museum, from Boll (no number), the pectoral girdle is well displayed (Text-fig. 17). The supracleithrum is a rather wide spatulate bone, but tapering to meet the cleithrum. Where the supracleithrum adjoins the cleithrum, there are two more bones of approximately the same size as one another, one is the postcleithrum and the other the extracleithrum. Both bones are oval in shape and there is very little ornamentation on them. The supracleithrum, postcleithrum, and extracleithrum all have a slight ridging on their posterior margins, but nothing to compare with the ornamentation of the other skull bones. The cleithrum is large and perfectly smooth, and this, together with the sparse ornamentation of the other girdle bone, suggest that the entire girdle was sunken and not exposed on the surface during life.

Nothing is seen of the other internal bones of the trunk because the squamation is thick and completely covers the skeleton. In specimen B.M.N.H. 19656 from Boll, the caudal region is reasonably clear, but there is no evidence of ossified vertebral rings and it appears safe to assume that the vertebral column was cartilaginous.

The pectoral fins contain stout fin rays which only articulate and divide distally. The more anterior rays are ornamented with fine longitudinal ridges of enamel, and show traces of small fulcra. The number of rays in the pectoral fin is between twenty-three and twenty-five.

The pelvic fins are smaller, and none of the lepidotrichia appears to be ornamented. There are from fifteen to twenty fin rays.

Unpaired fins. The dorsal fin arises well in front of the pelvics and has between eighteen and twenty-three fin rays.

Of the anal fin little trace can be found on any of the specimens examined in the B.M.N.H. The tail is hemiheterocercal and the scaly lobe short. The fin rays of the lower lobe are distantly articulated and finely divided distally.

Squamation. The body scales are highly ornamented and have been described at length in earlier works (see Aldinger, 1937 : text-figs. 85*b*, 87*b*). In the region of the pelvic fin three of the scales are modified ; these are ovoid in shape and considerably lengthened. They are narrowest posteriorly and twice the size of an ordinary scale. One or two of these modified scales also occur in front of the anal fin insertion. The course of the lateral line is marked by large clefts in the hinder ends of some of the scales it passes through, and its position is very low on the body wall. In particular, in one specimen in the Tübingen Museum, the course of the canal was marked by a pair of pores on each scale of the lateral line series, and occasionally an arcuate tubule.

Family SAURICHTHYIDAE

DIAGNOSIS. Elongate and slender fishes, with abbreviate-diphycercal tails. Dorsal fin far back, above the anal; the number of lepidotrichia in both exceeds that of the supporting radials. Radials of the dorsal fin either in one or two rows. Paired fins small. Radials of the pectoral fin only ossified in the Lower Triassic species, and the pelvic girdle is present as a distinct ossification only in the Triassic forms. Fulcra minute or absent. Long slender ribs present. Trunk wanting a continuous squamation, usually only four rows of scales, one dorsal, one ventral, and one lateral on either side supporting the lateral line, otherwise the body is naked (*Saurorhynchus brevirostris* (Woodward)). Maxilla of much the same shape as in the Palaeoniscoidea, firmly attached to the preopercular and the quadrato-jugal, and from within, to the ectopterygoid and dermopalatine. Hyomandibular is narrow and vertical, and without an opercular process. Quadrate and metapterygoid fused. The opercular apparatus consists of a single large opercular, but this bone possibly also incorporates a fused subopercular. Branchiostegal rays reduced, one on either side. Palate completely ossified, with paired vomers. The dentition consists of well-spaced, large conical teeth, with numerous intervening smaller teeth. Vomers and palate also bear teeth, but these are in the form of small rounded tubercles. Neurocranium completely ossified, with a large myodome, no basipterygoid process and no *processus craniospinalis*. There are two nasal orifices on either side and the supraorbital sensory canal passes between the two nasal openings. Head and opercular bones ornamented with striations and tuberculations. Notochord persistent, ossified vertebral elements are present in the Triassic forms, but absent in the Jurassic species.

REMARKS. This family contains two genera—the first *Saurichthys* Agassiz, into which all the Triassic forms are placed, and the second *Saurorhynchus* Reis, which contains only two species, both from the Lias.

Genus ***SAURORHYNCHUS*** Reis, 1892*b*

1844. *Belonostomus* Agassiz, 2, pt. 2, p. 142, pl. 47*a*, figs. 3, 4 (in part).
1858. *Belonorhynchus* (?) Bronn, p. 12 (in part).
1925. *Acidorhynchus* Stensiö, p. 175.
1940. *Gymnosaurichthys* Berg, pp. 194, 408.

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. *Saurorhynchus acutus* (Agassiz).

REMARKS. This genus was erected by Reis (1892*b* : 145) and incorporates the two Jurassic species, *S. acutus* (Agassiz) and *S. brevirostris* (Woodward). Berg (1940 : 194, 408) put the second species *brevirostris* into the new genus *Gymnosaurichthys* Berg, on account of its body being entirely naked. In almost every other respect *brevirostris* is very similar to *acutus* and I cannot agree with Berg (1940 : 194, 408) that the total absence of scales in the former is sufficient for the erection of a new genus *Gymnosaurichthys* for its reception.

The generic name *Saurorhynchus* was first used by Braun (1840 : 73) when he listed the species *Saurorhynchus tenuirostris*. When used by him it was a *nomen nudum*, but when Reis (1892*b* : 145) later used it to describe *Saurorhynchus acutus* the name became valid and as such must take preference over *Acidorhynchus* Stensiö (1925 : 175).

Saurorhynchus acutus (Agassiz)

(Text-figs. 19–22)

1844. *Belonostomus acutus* Agassiz, **2**, pt. 2, p. 142, pl. 47*a*, figs. 3, 4.
1844. *Belonostomus anningiae* Agassiz, **2**, pt. 2, p. 143 (name only).
1844. *Belonostomus tenellus* Agassiz, **2**, pt. 2, p. 143 (name only).
1858. *Belonorhynchus* (?) *acutus* (Agassiz) Bronn, p. 12.
1858. *Belonorhynchus* (?) *anningiae* (Agassiz) Bronn, p. 12.
1876. *Belonostomus acutus* Agassiz : Tate & Blake, p. 259.
1887. *Belonorhynchus acutus* (Agassiz) : Zittel, p. 222.
1888*a*. *Belonorhynchus anningiae* (Agassiz) : Woodward, p. 355.
1888*b*. *Belonorhynchus anningiae* (Agassiz) : Woodward, p. 147.
1890. *Belonorhynchus acutus* (Agassiz) : Woodward & Sherborn, p. 16.
1892*b*. *Saurorhynchus acutus* (Agassiz) Reis, p. 145 (in part).
1895*b*. *Belonorhynchus acutus* (Agassiz) : Woodward, p. 14, pl. 2, fig. 1.
1899. *Belonorhynchus acutus* (Agassiz) : Woodward, p. 456.
1921. *Belonorhynchus acutus* (Agassiz) : Hauff, p. 31.
1925. *Acidorhynchus acutus* (Agassiz) Stensiö, p. 175, fig. 58.
1938. *Acidorhynchus acutus* (Agassiz) : Hauff, p. 215.

DIAGNOSIS. A *Saurorhynchus* with a head between 10 and 15 cm. in length, and a maximum width of 10–15 mm. The height of the skull is usually from 20–30 mm., of which the mandible comprises approximately half. The head is from four and a half to five times as long as the maximum depth.

SYNTYPES. Fragmentary skulls (B.M.N.H. P 4268 and P 961*a*), both from the Upper Lias, Whitby.

MATERIAL. Specimens in the B.M.N.H., the Sedgwick Museum Cambridge, the Oxford and Geological Survey Museums.

REMARKS. Although the types came from the Upper Lias of Yorkshire, all the remaining specimens in the B.M.N.H. are from the Lower Lias of Lyme Regis.

DESCRIPTION. *The skull.* The dermal roof is a completely fused shield, with individual bones very difficult to make out.

Stensiö (1925 : 89) found in the genus *Saurichthys* indications of a set of bones in front of the frontals, and more or less embedded in the roof of the rostralo-premaxillary. He was not sure of their true extent, but called the bones anterior postrostral elements which included the interrostrals. Two specimens of *Saurorhynchus acutus* (one in the Geological Survey Museum No. 492, the other from the Sedgwick Museum, Cambridge) show clearly the extent of these bones. There is quite definitely a pair which abuts not only on to the frontals as Stensiö (1925 : 89) supposes, but also on to the nasals (Text-fig. 19). I have called this pair of bones, which extends about three-eighths of the way along the rostrum, the interrostrals.

The paired frontals extend from in front of the nasals back almost to the posterior margin of the orbit. Stensiö (1925 : 89) thinks that on account of the considerable

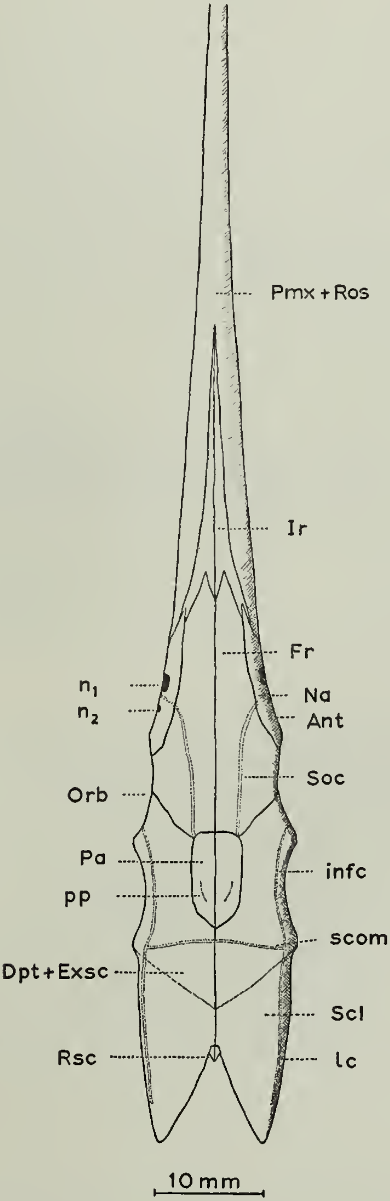

FIG. 19. *Saurorhynchus acutus* (Agassiz). Skull roof, reconstructed, dorsal view.

extension forward on to the ethmoidal region, the frontals probably also include the homologue of the posterior postrostral elements of the Rhipidistids. Anteriorly the frontal bounds the nasal, antorbital and the interrostrals, but it does not come into contact with the rostralo-premaxillary as in *Saurichthys* (Stensiö, 1925 : 89). Posteriorly the frontals do not extend far enough round the orbit to meet the dermosphenotic (Text-fig. 20). The posterior edge of the frontals is fused to the parietals. In both *Saurorhynchus acutus* and *Saurorhynchus brevirostris* there is only one pair.

These parietals are small and form a comparatively tiny heart-shaped bone in the centre of the cranium, just to the rear of the orbits. Occurring on the surface of each parietal is a short line of pit organs similar to those of *Saurichthys*.

The rest of the cranial roof is composed of a sheet of bone of composite nature, containing the dermopterotic-extrascapular series. This sheet at its anterior end bounds the posterior edge of the orbits, the frontals and the parietals. It continues backwards beyond the opercular on either side. The lateral edge of the sheet is, after it leaves the orbit, distinctly concave, then further back it becomes convex (Text-fig. 19). The dermopterotic-extrascapular portion of the shield appears to have a suture line running back across it towards its posterior end, just behind the supratemporal commissure. This suture is indistinct, but runs backwards on either side meeting in the mid-line, midway between the parietals and the first ridge scute.

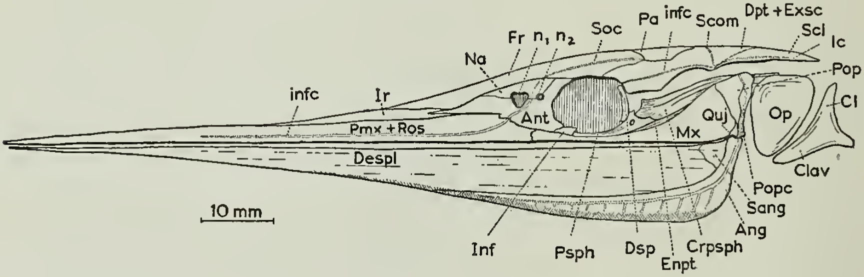

FIG. 20. *Saurorhynchus acutus* (Agassiz). Reconstruction of skull in lateral view.

The remaining portion of the shield extends backwards on either side to a point beyond the cranio-spinal process. It probably contains the suprascapular and the supracleithrum fused indistinguishably together. At its centre posteriorly it contains a small triangular bone, which is the most anterior dorsal ridge scute.

The ornamentation of enamel of all these bones including parietals, rostrals, frontals etc., is coarser than that found on the rest of the skull, and consists mainly of short stout striae. These run in a more or less longitudinal direction on the parietals, frontals and dermopterotic-extrascapular, whilst on the nasals they radiate downwards.

The orbit is large and while there is evidence in some specimens of a complete sclerotic ring, this appears not as a truly ossified bone but rather in the form of a calcified cartilage. The bones of the cheek and the infraorbital series do not often appear to be preserved, but by mechanical preparation of a few of the B.M.N.H. specimens some of the structures have been revealed.

In no specimen was a supraorbital bone located, but by analogy with other Saurichthyids and related forms, it must be assumed that either one or more supraorbital was present during life and that due to conditions of fossilization has since been lost. However, a small infraorbital bone occurs near the base of the orbit, abutting on the posterior ventral surface of the antorbital, and having every appearance of Stensiö's lachrymal (Text-fig. 20), while bounding the posterior margin of the orbit, a well-developed dermosphenotic can be seen. The dermosphenotic is a curved bone which does not fit neatly on to the skull roof, suggesting thereby the absence of another bone series—the supraorbital.

As with the supraorbital, the remaining infraorbitals are also missing. What Woodward (1895*b* : 16) describes as a suborbital is a narrow bone beneath the orbit, but in reality this is only the anterior portion of the parasphenoid. When fully prepared, in every case this narrow bar-like bone extended backwards, and always a large foramen became visible in it. This foramen is for the external carotid artery, which proves the bone to be the parasphenoid and not the suborbital.

The parasphenoid in the region of the floor of the orbit exhibits a strong convexity ventrally, but as it continues backwards it fuses with neurocranial elements, and is a ridged bar beneath the cranial shield and often extending beyond it.

It is true to say that the orbital series of bones was less well ossified than the surrounding dermal bones, and as a result is rarely preserved.

According to Woodward (1895*b* : 10, 16), the nasal opening is single on each side, and obliquely elongated. Stensiö (1925 : 90), however, has shown that in *Saurichthys* there are two nasal vacuities. On examination of *Saurorhynchus acutus* and *S. brevirostris* this also proved to be the case, the anterior nasal aperture being the larger of the two.

Stensiö (1925 : 90) called the bone containing these two apertures the nasalo-antorbital, because he recognized that it was formed as a result of the fusion of two bones (cf. Rhipidistid Crossopterygians). In one specimen of *Saurorhynchus acutus* in the B.M.N.H., the nasalo-orbital was clearly shown to consist of two bones, the nasal and the antorbital. Both bones were seen to enter into the formation of the apertures, the nasal forming the top half of the anterior nasal aperture and the antero-dorsal part of the posterior nasal aperture, the remaining portions of the apertures being bounded by the antorbitals (Text-fig. 20).

The maxilla is the same shape as that found in the Palaeoniscids, and is firmly fused on to the premaxilla. At its posterior end the maxilla unites with the preopercular, the suture line between them being almost obliterated. Both Stensiö (1925, fig. 21) and Woodward (1895*b* : 10) observed the maxilla, but Stensiö also recognized a preopercular. In neither *Saurorhynchus acutus* nor *S. brevirostris*, was it possible to establish with certainty whether or not a quadrato-jugal was present. The maxilla continues forwards and forms a thin bar beneath the orbit and fuses with the premaxilla just anterior to the orbital foramen. Interiorly the maxilla fuses with the ectopterygoid and dermopalatine. The quadrato-jugal is, however, present and is observable from the side as a very small triangular bone set between the posterior ventral corner of the maxilla and the anterior ventral corner of the preopercular. Together with the preopercular it enters into the jaw articulation.

The preopercular is smaller than the maxilla and is triangular in shape. It has a pronounced ridge running in a vertical direction near to its posterior edge. Behind this ridge the preopercular sensory canal travels upwards from the articulatory facet to the top of the preopercular. The posterior and anterior edges of the bone are slightly concave and approximately equal in height. Both the maxilla and the preopercular exhibit a strong rugosity similar to that found on the frontals and parietals.

Immediately behind the preopercular, although not actually in contact with it, is the opercular. The opercular is very much smaller than in the rest of the Saurichthyids. In shape it is deeper than broad, and there is no indication of its being succeeded by any branchiostegal rays. The ornamentation of the opercular consists of short striae which radiate outwards and downwards from the anterior dorsal corner.

The much elongated rostrum appears to be formed chiefly of one bone as in *Saurichthys* (Stensiö, 1925 : 89)—the rostralo-premaxilla. Running three-quarters of the length of this composite bone is a branch of the supraorbital sensory canal. The supraorbital canal presumably continues on up between the two nasal foramina as in *Saurichthys*.

Lower jaw. The lower jaw is just a little shorter than the upper, both being elongated forwards, and tapering strongly to their anterior extremities. The mandible is deepest posteriorly, its posterior border descending almost vertically from its articulation with the skull. This border is in most cases concave, whereas in *Saurichthys* it is normally convex.

The Meckelian cartilage is ossified and the outer surface is covered by three dermal bones, the angular, surangular and dentalo-splenial ; whilst on the inside is a long mixicoronoid (terminology from Stensiö, 1925). Since a double series of large teeth (B.M.N.H. P 965*b*) extends to the termination of the mandible, there can be no pre-symphysial bone.

The angular is the most posterior bone, and its hinder border descends in a slightly concave manner from the articulation with the upper jaw. This has the effect of making the deepest region of the mandible the most posterior. Along the length of the angular bone runs a branch of the sensory canal system (mandibular branch), but here it differs from that condition found in the other Saurichthyids in that it sends off ventrally numerous fine branches, which give the appearance of a series of vertical striations. This mandibular canal can be traced back through the jaw articulation and up into the preopercular. The angular participates directly in the mandibular articulation to the exclusion of the surangular. At its anterior end it tapers almost to a point, and its demarcation is clearly visible as it runs from the most dorsal posterior point in a strong concave sweep until it reaches this anterior extremity.

The surangular is a small bone which abuts the angular in the posterior dorsal region, and forms for a short distance the dorsal edge of the jaw. This bone is triangular in shape and fuses indistinguishably into the dentalo-splenial, which actually covers part of its anterior surface.

The dentalo-splenial forms the long tapering anterior portion of the mandible. Posteriorly it meets the angular along its ventral edge, whilst dorsally it abuts on to and over the surangular.

The ornamentation of the lower jaw generally consists of a superficial rugosity, not so well marked as that found on the dermal bones of the skull roof. The ornamentation on the angular bone runs in a vertical direction, while that on the dentalo-splenial is only found at the posterior end where it is horizontal.

Dentition. The dentition on the margin of both jaws is essentially similar. The teeth fall into two series and all are capped with enamel. Those comprising the larger series vary in height from 2–5 mm., those of the smaller series from 0·5–1 mm. The larger teeth are conical, pointed and curved backwards. Occurring in both the upper and lower jaws is a series of notches (Text-fig. 21) for the reception of the larger teeth of the opposite jaw. The notches and teeth alternate and allow the jaws to be tightly closed. The intermediate spaces between the larger teeth are filled with the small-tooth series. These are thin, sharply pointed and more numerous than the larger ones. The two sets occur along the whole length of the ventral surface of the rostralo-premaxillary and on to the anterior portion of the maxilla. On the lower jaw they occur along the dorsal edge of the dentalo-splenial almost up to the surangular.

The vomers and the anterior region of the parasphenoid are also provided with small teeth of a more rounded, almost stud-like variety. The mixicoronoid has teeth of even smaller size on some of its surface. In the large tooth-series the teeth get more robust posteriorly, and many show an absence of vertical striations basally of the enamel cap (Text-fig. 22). The dentition strongly suggests that the genus had a predaceous habit.

Neurocranium. An ossified neurocranium is present, both Woodward (1895*b* : 10) and Stensiö (1925 : 176) being in error in assuming that it was cartilaginous (Text-fig. 21).

The neurocranium forms one single ossification, there being no individual bones recognizable. The endocranium on the one specimen (G.S. 492) which I was able to prepare in acetic acid (Text-fig. 21), was unfortunately a little broken up in the optic region. However, several foramina could still be distinguished. I think the fenestra optica was much larger in this species than in the other Saurichthyids (Stensiö, 1925), the roof of it showing three foramina on either side.

The most anterior foramen was for the exit of nerve I, whilst that one immediately below and to the posterior of it was for the exit of a blood vessel. The foramen in this case has a groove running anteriorly from it with several small foramina within that groove. From its position this blood vessel must have been the *vena cerebralis anterior* (*vert.cart.ant.*). Above the canal for this vessel occurs another small foramen, and by analogy with other Saurichthyids (Stensiö, 1925) this must have been the exit for nerve IV.

The optic and other adjoining foramina are missing, but a distinct trigemino-facialis chamber occurs just anterior to the *processus ascendens* of the parasphenoid. On the same level as the trigemino-facialis chamber, but nearer to the edge of the neurocranium occur two more foramina, somewhat separated from the more posterior

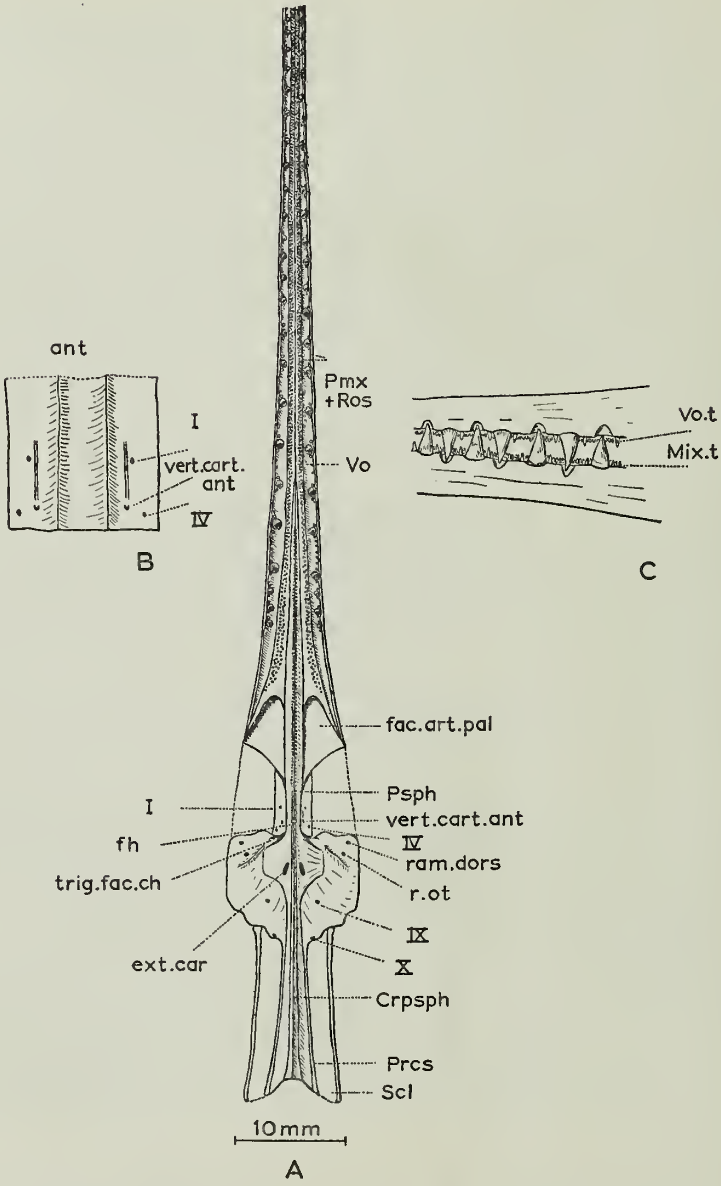

FIG. 21. *Saurorhynchus aculus* (Agassiz). A, Neurocranium and palate, ventral aspect, from G.S. 492. B, Optic region of same specimen, ventral view, parasphenoid removed. C, Small portion of jaw of another specimen to show alternation of teeth and notches.

foramina by a distinct ridge. The more anterior of the pair transmitted branches of the *r. ophthalmicus superficialis trigemini* (*ram.dors.*), whilst the posterior member (*r.ot.*) transmitted the *ramus oticus*.

Only two further foramina were located, both well back on the neurocranium. The first was the exit for nerve IX and the more posterior for that of nerve X.

The occipital region is long and relatively narrow, being widest most posteriorly where it broadens somewhat to form the cranial spinal processes. It is covered very nearly completely throughout its length by the parasphenoid.

Of the other bones of the skull little is observable. The hyomandibular (Sedgwick Museum J 36707) is long and in an oblique position, somewhat broadened antero-dorsally, its axis being much inclined forwards, occupying a similar position to that found in the Palaeoniscids. Covering the dorsal end of the hyomandibular is a small ossification here called the dermohyal. This bone is more posterior in position than the bone Px of Stensiö (1925 : 92), fitting between the dorso-anterior end of the maxilla and the dermopterotic-extrascapular. Ossified elements such as the autopalatine, entopterygoid, ectopterygoid and dermopalatine are also present. The entopterygoid only is visible on most of the specimens. From within the ectopterygoid and dermopalatine are firmly united with the maxillae.

Palate. In the palate the paired vomer is a long narrow bone traversing the whole length of the underside of the rostrum (G.S. 492). At its posterior end it is separated into its two constituent bones by the intervention of the parasphenoid (Text-fig. 21). The parasphenoid stretches about one-third of the distance up the vomers and where it ends the two vomers are divided by a suture for the remaining two-thirds of their length. Consequently the vomer is widest posteriorly, the two ends diverging to border the articulatory surface for the reception of the autopalatine.

The parasphenoid itself extends posteriorly from the vomers right back over the occipital region of the neurocranium. The anterior portion of this bone is dagger-shaped, and as it continues back over the orbital region it narrows somewhat. In this area it is pierced by the *fossa hypophyseus*. Immediately behind the fossa the parasphenoid fans out into the *processus ascendens*, which covers a large portion of the labyrinth region of the underlying neurocranium. The true extent of the *processus ascendens* is difficult to ascertain since the bone is very much broken in this area. However, the canal on either side for the external carotid artery is clearly discernible. Posteriorly to the *processus ascendens* the parasphenoid again narrows and exhibits a distinct crest, but as it continues on back over the occipital region the bone expands and becomes much wider posteriorly, whilst the crista becomes less pronounced and finally tapers out. The parasphenoid extends so far back in this species that it covers a portion of the lower side of the most anterior vertebra.

Sensory canals. The supraorbital sensory canal has its origin posteriorly at a point where the frontals fuse with the parietals. It then runs forward on either side and passes down between the two nasal vacuities to fuse with the infraorbital canal. From below the antorbital the supraorbital canal runs about three-quarters of the length of the rostralo-premaxillary. The other portion of the infraorbital canal forms a direct continuation of the cephalic portion of the lateral line. Thus the two together form a canal on either side of the posterior head shield, which runs from the orbit back to the posterior end of the shield (Text-figs. 19, 20). Its forward continuation down through the dermosphenotic cannot be traced, mainly because of the bad state of preservation of the latter. The two cephalic portions of the lateral line of each side are joined by the supratemporal commissure. This passes across the dermopterotic-extrascapular. Finally, the course of the mandibular which is a direct continuation of the preopercular canal has already been described.

The similarity between this system and that found in the Palaeoniscids has already been pointed out by Stensiö (1925 : 213).

Appendicular skeleton. No remains of the skeleton of the unpaired fins have been found, although some traces of the paired fins can be seen. Immediately behind the opercular in several specimens occurs a triangular-shaped bone with its edges facing ventrally, caudally and antero-dorsally. This bone is the fused cleithrum and clavicle and served for the articulation of the pectoral fin.

Axial skeleton. The notochord was persistent, and the neural and haemal arches much expanded, both bearing spines. In the caudal region the short slender neural spines become elongated to be symmetrical with the haemals. In no specimen is there satisfactory indication of intramuscular bones.

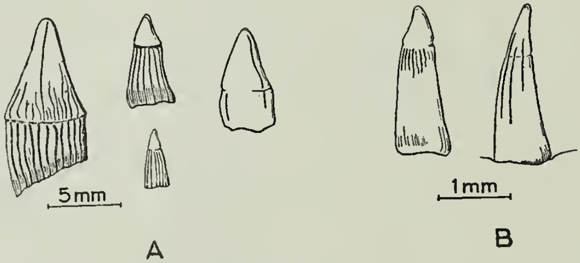

FIG. 22. A, Teeth of *Saurichthys* sp. B, Teeth of *Saurorhynchus acutus* (Agassiz) to show variation in striation.

Squamation. The body appears to have been covered with only four rows of bony scutes, one dorsal, one ventral and one lateral on either side (supporting the lateral line).

Systematic position. The genus *Saurorhynchus* (*Acidorhynchus*) according to Stensiö (1925 : 175) differs from *Saurichthys* in the following respects :

> " 1. Smaller lengthening of the rostrum.
> 2. No or very slight ganoine ornamentation.
> 3. Certain differences in the shape and relations of the dermal bones.
> 4. Rather much reduced opercular.
> 5. Absence of vertical striations on the teeth basally of the enamel cap."

I have examined the above points and find that only two of the five are valid differences. Taking them in order, first the " smaller lengthening of the rostrum ": measurements were made on all the skulls of *Saurichthys* and *Saurorhynchus* that were available, and a direct comparison made in each case of the length of the rostrum against the length of the rest of the head. Plotting these measurements graphically, both genera fall on the same straight line (Text-fig. 80), and there is no significant difference in the relative length of the rostrum between the two.

The second difference, " no or very slight ganoine [enamel] ornamentation " is also incorrect, since all the skull roofs of *Saurorhynchus* that I have examined show an ornamentation, in some cases quite thick, of tubercles and striae of enamel. The third and fourth differences, " certain differences in the shape and relations of the dermal bones " and a " rather much reduced operculum " are perfectly valid. By comparing the above description with those given by Stensiö (1925) and Lehman (1952) for the earlier genus *Saurichthys*, these differences will be apparent. The reduced opercular is particularly noticeable. Finally, the " absence of vertical striations on the teeth basally of the enamel cap " in the genus *Saurorhynchus* is incorrect. Several teeth of *Saurorhynchus* I have examined show striations basally of the enamel cap (Text-fig. 22), whilst others of *Saurichthys* show an absence of such striations (Text-fig. 22).

Although three of Stensiö's (1925 : 175) five reasons for founding the genus *Acidorhynchus* are no longer valid, the two remaining, plus such features as a less heavily ossified neurocranium in *Saurorhynchus* and the absence of intramuscular bones and ossified pelvic girdle, and the peculiar pectoral girdle, make the retention of the genus necessary to incorporate the Liassic species *acutus* and *brevirostris*.

" HOLOSTEI "

Family FURIDAE

DIAGNOSIS. See Woodward, 1895*b* : 285. (EUGNATHIDAE).

Genus ***OSTEORACHIS*** Egerton, 1868

DIAGNOSIS. Trunk elongate, paired fins large, but pectorals considerably larger than pelvics. Dorsal fin opposite the pelvic fins, the anal fin immediately behind the pelvics. Dorsal and anal fins triangular and the caudal fin deeply forked. Fulcra present on all the fins, distal articulations of the lepidotrichia very close. Opercular much larger than the subopercular. Dentition : marginal teeth large, well spaced and slightly curved. Teeth on the splenial and ectopterygoid smaller, long and slender. Distinct pleuro- and hypocentra. External skull bones ornamented with tubercles and striae of enamel. Scales thin possessing distinct peg-and-socket articulations.

TYPE SPECIES. *Osteorachis macrocephalus* Egerton.

REMARKS. Three species only of this genus have been described, *Osteorachis macrocephalus* Egerton and *Osteorachis granulata* Egerton both from the Lower Lias of Lyme Regis, and *Osteorachis leedsi* Woodward, from the Oxford Clay of Peterborough.

Osteorachis macrocephalus Egerton

(Text-figs. 23–27)

1839. *Pachycormus ? macrurus* Agassiz, **2**, pt. 2, p. 113, pl. 58*a*, fig. 3.
1868. *Osteorachis macrocephalus* Egerton, p. 500.
1872. *Osteorachis macrocephalus* Egerton : Egerton, no. 5, pl. 5.
1876. *Harpactira* (*Harpactes*) *velox* Egerton, pp. 441, 576.
1885. *Heterolepidotus grandis* Davis, p. 293, pl. 7.
1890. *Harpactira velox* Egerton : Woodward & Sherborn, p. 92.
1890. *Osteorachis macrocephalus* Egerton : Woodward & Sherborn, p. 136.
1890. *Platysiagum grandis* (Davis) Woodward & Sherborn, p. 151.
1895*a*. *Osteorachis macrocephalus* Egerton : Woodward, p. 204, pl. 7, fig. 10.
1895*b*. *Osteorachis macrocephalus* Egerton : Woodward, p. 325.
1897. *Osteorachis macrocephalus* Egerton : Woodward, p. 385.

DIAGNOSIS. An *Osteorachis* of large size reaching up to a metre in length. The length of the head is about a quarter of the total length of the fish. The body is fusiform, approximately seven times as long as deep. Opercular considerably deeper than broad, much larger than the subopercular. The latter is at least three times as broad as deep. Scales finely and closely tuberculated. Neurocranium heavily ossified.

SYNTYPES. B.M.N.H. P 3654, P 3655, P 3649 and P 3648*a*, from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H. and the University Museum, Oxford.

REMARKS. Agassiz (1839 : 113, pl. 58*a*) described an imperfect tail from the Lower Lias, Lyme Regis as *Pachycormus ? macrurus*. This specimen is now in the Oxford Museum (No. J 3050). I have examined the specimen but find that its relationship to the genus *Osteorachis* is not certain. If in fact it can be proved subsequently to be the tail of an *Osteorachis*, then the species *Osteorachis macrocephalus* Egerton is no longer valid, and the name *Osteorachis macrurus* (Agassiz) would take preference, with this specimen as holotype.

DESCRIPTION. *The skull*. The skull roofing bones are well preserved in B.M.N.H. P 875. This is a small specimen, probably of a young individual on which the suture lines are still clearly marked. On the large skull of B.M.N.H. P 3648*a* only the demarcation between the frontals is at all clearly shown.

The frontals are by far the largest of the bones forming the skull roof (Text-fig. 23). They are much the same width along their entire length, although they narrow somewhat anteriorly. The median suture line is well shown, being characteristically wavy, with one large acute lobation posteriorly. Behind the frontals are the much smaller parietals. These are remarkably asymmetrical, and, like the other skull bones, are covered with a coarse tuberculation. Posteriorly the frontals are in contact with the dermosphenotics which, although smaller than the other skull roofing bones, are large in comparison with those found in *Caturus* and other allied genera. The remaining roofing bones making up the posterior portion of the skull are the dermopterotics. These are much longer than the parietals and form a distinct edge to the roof in that region. They abut on the parietals, frontals and dermosphenotics on their inner margins. The remaining bones represented in B.M.N.H. P 875 are those seen posterior to the parietals, and are the extrascapulars, not displaced otic bones, as Woodward (1895*b* : 328) erroneously described them. The roofing bones of the snout are more difficult to interpret, no one specimen showing them *in situ*. However in a specimen in the Oxford Museum (Ox. M. J 3033), a small somewhat displaced bone near the anterior end is probably a nasal (Text-fig. 24). By comparison with *Caturus* it is reasonable to suppose that a pair of nasals did in fact occur anteriorly to the frontals.

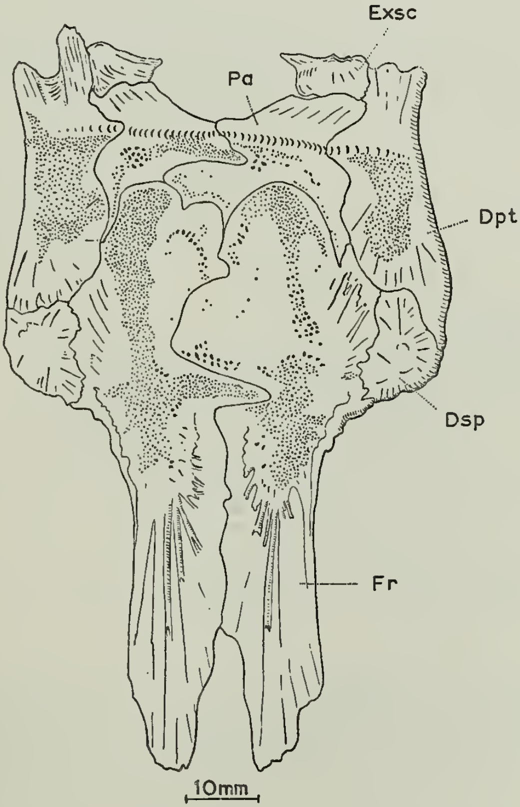

FIG. 23. *Osteorachis macrocephalus* Egerton. Dorsal view of skull roofing bones. From B.M.N.H. P 875.

Specimen Ox. M. J 3033 is more or less laterally compressed, and much fractured and crushed, although the left orbital surface has remained practically intact. From this specimen much of the cheek bone arrangement can be derived. However, the region represented is that anterior to the opercular apparatus, and specimens B.M.N.H. P 876*x* and P 3648 must be examined to show the latter.

The premaxilla is a small bone bearing from eight to ten closely set teeth, of much the same appearance as those found on the maxilla. A fragment of bone appearing above the premaxilla is undoubtedly the remains of a rostral bone. The maxilla is a long slender bone, thickened anteriorly and deepened behind. The tooth arrangement on this bone is of interest since one of the generically distinguishing features between this species and *Furo* is the enlargement of the inner clustered teeth. In specimen Ox. M. J 3033 Woodward (1895*a* : 205) maintained that the maxilla and mandible bore only a single series of teeth, and that the cluster of teeth appearing below the maxilla pertained to the ectopterygoid, whilst those above the dentary to the splenial. By acid development I have been able to show that this is incorrect, as on both the upper and lower jaws there are often two to three rows of teeth.

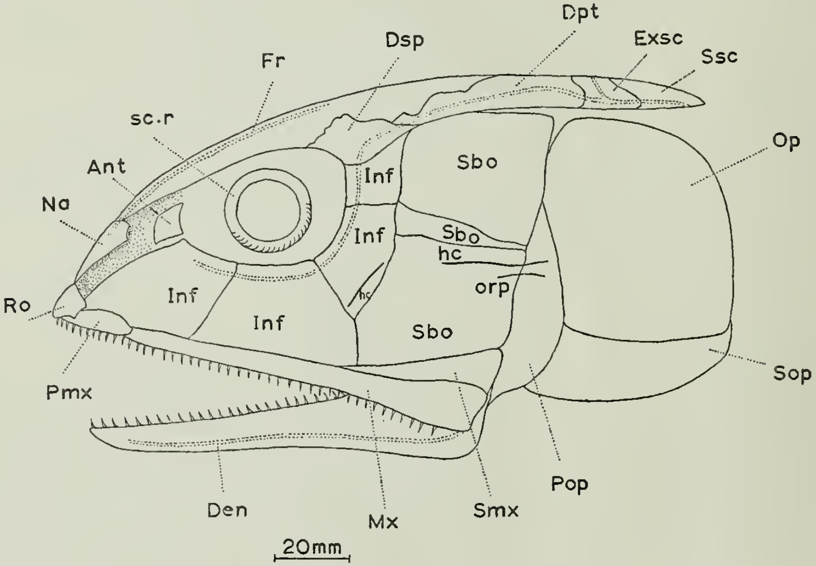

FIG. 24. *Osteorachis macrocephalus* Egerton. Reconstruction of the dermal bones of the skull in lateral view.

The outer teeth are long, slender, hollow and pointed, the inner ones being similar in shape, but smaller. These inner teeth are not very much different from those covering the ectopterygoid and splenial. The fact that most of the palatal bones are covered by teeth makes the total absence of teeth on the parasphenoid difficult to understand. Above the posterior margin of the maxilla a single supramaxilla occurs. This is a small bone, distinctly pointed at its anterior end.

Immediately in front of the preopercular two fair sized bones can be seen, one above the other, with a smaller one separating them. These represent the suborbital series. They are very similar in proportion to those found in *Caturus*, the similarity in the respective cheek bones of these two genera being striking.

The opercular itself is a large bone rounded above and deeper than wide. It is covered externally with a fine and close tuberculation, with areas of large tubercles interspersed. The subopercular beneath is more drawn out, being much wider than deep (cf. P 3648). The preopercular separating these two bones from the orbital series is a longer, thinner, much curved bone, similar to that found in the genus *Caturus*.

The orbit has a completely ossified sclerotic ring, around which fragments of further ossification are to be seen. These fragments represent the intraorbital series so characteristic of the Holostei. This series consists of five plates. The two posterior ones are small, and form together the hinder edge of the orbit. The two ventral plates are much larger, approximating in size to those of the suborbital series. They form the lower margin of the orbit and extend down on to the maxilla. The last plate only remains as a fragment, but obviously completed the margin of the orbit anteriorly. This fragment is termed a prefrontal by Woodward (1895*a* : 205) but is more probably an antorbital.

Lower jaw. The lower jaw is intact in Ox. M. J 3033 except for its posterior extremity. It shows a high coronoid process and the general shape of the jaw can be followed. The quadrate is represented in B.M.N.H. P 3654 and is relatively large with a well-developed articulatory process for the lower jaw. The hyomandibular is seen in B.M.N.H. P 3654 and has a long opercular process. This process is somewhat unusual in that it has a thin sheet of bone connecting both its upper and lower extremities with the hyomandibular proper. Returning to Ox. M. J 3033, between the rami of the mandibles a complete gular plate is observable, two-thirds as long as broad with a normal series of branchiostegal rays behind it.

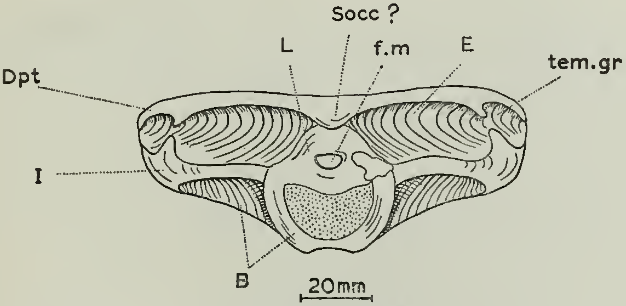

FIG. 25. *Osteorachis macrocephalus* Egerton. Hind view of neurocranium. From B.M.N.H. P 3648*a*.

Neurocranium. Beneath the dermal roof is a remarkably well-ossified neurocranium, much heavier and stouter than in any other species of Holostean fishes I have examined. The following account is based on one specimen (B.M.N.H. P 3648*a*), the few other specimens of the species known being all completely flattened and thus unsuitable for acid development.

The general shape of the neurocranium differs considerably from that of the other Holostei. It is almost twice as broad as deep, thereby giving the whole neurocranium a much flattened appearance. The ossification is complete, as in *Dapedium*, there being no remnants of cartilaginous areas. Consequently suture lines are almost obliterated and careful study is needed to interpret the demarcation of the various bones.

This task is the most difficult in the postorbital region. A backwardly and downwardly directed projection above the foramen magnum I interpret as a supraoccipital (Text-fig. 25), but since no suture lines are visible I do so with reservation. From its position the bone around the foramen magnum is presumably the lateral occipital, which together with the epiotics, make up the rest of the neurocranium in this region. Abutting on the epiotics and lateral occipitals is a large and well-defined intercalar. This forms the base of the temporal groove, which in this species is long and well developed, giving a large surface area for the insertion of the trunk muscle ligaments. The provision of such broad and large grooves reflects the size of the muscles necessary to compensate the very heavy skull.

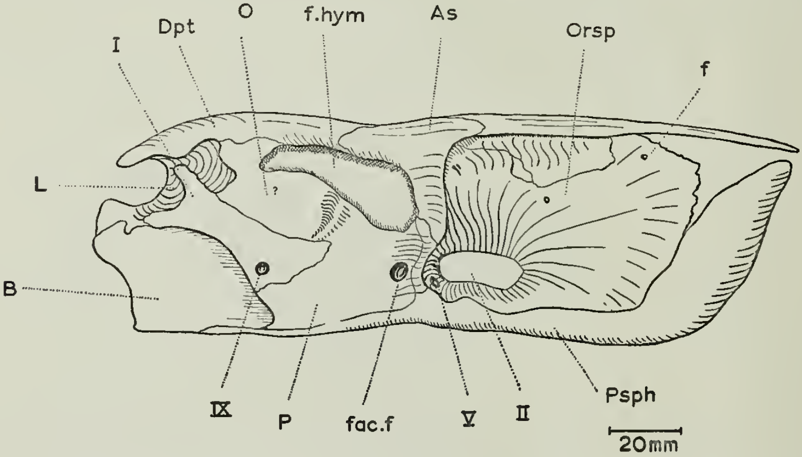

Fig. 26. *Osteorachis macrocephalus* Egerton. Neurocranium in lateral view. From B.M.N.H. P 3648*a*.

The basioccipital is a stout bone bordering the notochordal pit, and contributes to the formation of the lateral wall of the neurocranium. The intercalar too forms part of the lateral wall and the suture lines between it and the surrounding bones are well shown (Text-fig. 26). From the ventral region of the intercalar arises the ninth nerve. Dorsally this bone extends back into an irregular projection, similar to that described by Rayner (1948 : 292) in *Caturus*, for the attachment of ligaments from the suprascapular. The remainder of the lateral wall in the postorbital region is made up of the prootic and opisthotic. The opisthotic is quite large and bears the posterior half of the hyomandibular facet, besides forming the wall of the otic capsule. The prootic covers a larger area than the opisthotic and posteriorly is indented to take the anterior half of the hyomandibular facet. The most anterior portion of the facet is borne by the autosphenotic. Only one recognizable foramen is found in the prootic, the so-called facial foramen. This foramen transmitted the hyomandibular branch of the facial nerve.

The orbital surface is relatively easy to interpret (Text-fig. 27). The autosphenotic forms a large portion of the dorso-lateral region. The extent of the other orbital bones, pterosphenoid, prootic, basisphenoid and orbitosphenoid, can all be seen from Text-fig. 27. The optic foramen is large and confluent with the infra-orbital fenestra. There is a complete bony interorbital septum, with several foramina near its anterior end. The myodome is large, its two orbital openings being separated by the narrow stem of the basisphenoid. The cavity of the myodome extends back for about 2 cm. and is walled by the prootic and basisphenoid, whilst the floor is formed by the parasphenoid. Near its anterior end the roof bears an entrance for the hypophysis.

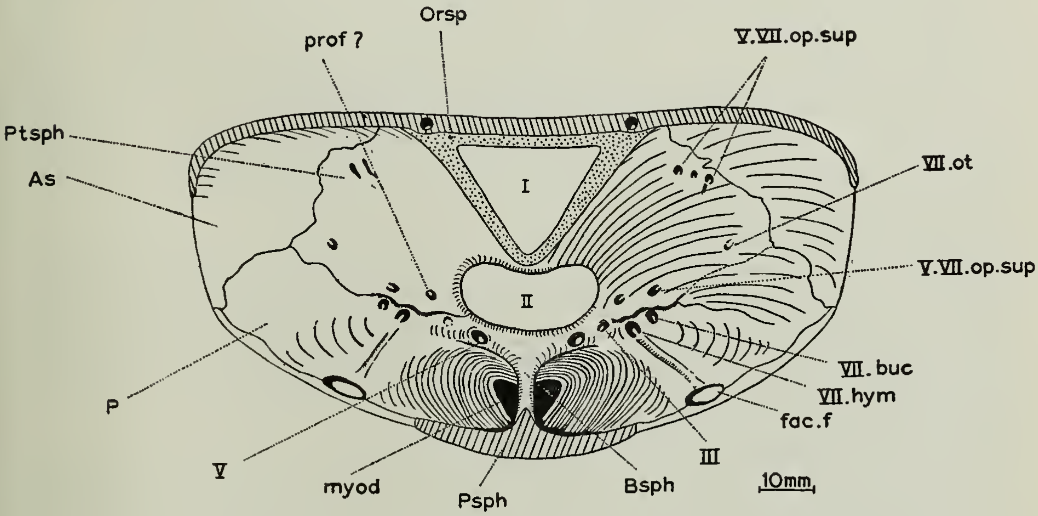

FIG. 27. *Osteorachis macrocephalus* Egerton. Neurocranium as if cut vertically just anterior to the optic foramen, showing the orbital surface. From B.M.N.H. P 3648*a*.

There is no true facial chamber as in *Caturus*. The main branch of the trigeminal has a fairly large foramen, in a similar position to that seen in *Caturus* (Rayner, 1948, fig. 7). Slightly dorsal to V is a smaller foramen, which transmitted the oculomotor nerve. From this last foramen a distinct ridge runs for some distance towards the lateral edge of the orbital surface. This ridge probably represents the demarcation between the pterosphenoid above and the prootic beneath. Under this ridge occur two more foramina, the larger one serving in life to transmit the hyomandibular branch of the VIIth, which passes down through the facial foramen. A well-marked canal can be seen running between the exit of the hyomandibular and the facial foramen. Beyond the foramen for the hyomandibular lies the other smaller foramen and this transmitted the buccal branch of the VIIth. The pterosphenoid bears several foramina. Of these, the one nearest the optic foramen possibly served for the exit of the profundus. Continuing outwards, the next upwardly directed foramen served for the passage of the superficial opthalmic. Towards the roof of the orbit and still in the pterosphenoid are several smaller foramina. These downwardly directed foramina were for the secondary branches of the superficial ophthalmic, supplying sensory organs (neuromasts). The remaining foramen in the pterosphenoid is that furthest from the mid-line, and was probably for the exit of the otic branch of the facial nerve.

The parasphenoid is a much broadened bone in this species (Text-fig. 26). It extends posteriorly on to the basioccipital which forms the floor of the neurocranium in that region. Passing forwards, the parasphenoid still maintains its broadened form and curves sharply upwards to meet the skull roofing bones. The absence of teeth of any type on the parasphenoid seems peculiar since this form has every appearance of a carnivorous feeder.

Sensory canal system. The course of the supraorbital canal can be traced on the frontals of B.M.N.H. P 875. It runs along the middle of each bone, and gives off a series of smaller radiating canals which pass out from it over the anterior surface of the frontal. The supraorbital canal continues on down into the nasals. The infraorbital canal can only be traced for a short distance through the anterior edges of the two posterior infraorbitals (Text-fig. 24), but the mandibular canal can be traced the length of the dentary.

Both the postmaxillary and supramaxillary sensory lines can be seen on Ox. M. J 3033. The supramaxillary line starts on the preopercular and runs forward across the dorsal region of the third suborbital. The anterior division of this sensory line runs more obliquely downwards through the surface of the postero-ventral corner of the second infraorbital. The postmaxillary line commences just below the supramaxillary line, in the preopercular and it only runs for a short distance into the posterior dorsal region of the third suborbital.

Appendicular and axial skeleton. As with most of the Holostei, the vertebrae are not completely ossified, there being distinct hypo- and pleurocentra. The fins are identical in general character with those of *Furo*, and there is little to be added to previous descriptions. The pectoral girdle is not shown on any of the specimens I have examined, but on B.M.N.H. P 3655 the pelvic girdle is well displayed. It consists of two bones, one somewhat displaced. These bones are not large, and are expanded posteriorly, but I can see no resemblance to an " hour-glass " shape attributed to them by Woodward (1895*b* : 327).

Squamation. The scales exhibit peg-and-socket articulation, and the ornamentation is rather characteristic. Often they are covered in tubercles which on some of the abdominal scales pass into conspicuous striae on the posterior halves.

Genus ***HETEROLEPIDOTUS*** Egerton, 1872

1861. *Brachyichthys* Winkler, p. 47.
1868. *Eulepidotus* Egerton, p. 505.

DIAGNOSIS. Holostean fishes of moderate size, hardly distinguishable from *Furo*. They differ from *Furo* in having a more deeply fusiform body and smaller teeth on the dentary and maxilla. Further, the vertebral elements are more heavily ossified in *Furo* than in all but the smallest species of *Heterolepidotus*. The squamation also differs in the two genera, *Furo* having pectinated scales, while those of *Heterolepidotus* are serrated but not normally pectinated.

TYPE SPECIES. *Heterolepidotus rhombifer* (Agassiz).

Heterolepidotus rhombifer (Agassiz)

(Text-figs. 28–30)

1836. *Semionotus rhombifer* Agassiz, **2**, pt. 1, p. 228, pl. 26*a*.
1837. *Lepidotus fimbriatus* Agassiz, **2**, pt. 1, p. 247, pl. 33*b*.
1849. *Lepidotus fimbriatus* Agassiz : Williamson, p. 444.
1849. *Semionotus rhombifer* Agassiz : Williamson, p. 444, pl. 41, fig. 9.
1868. *Eulepidotus fimbriatus* (Agassiz) Egerton, p. 505.
1872. *Heterolepidotus latus* Egerton, no. 2, pl. 2.
1887. *Heterolepidotus fimbriatus* (Agassiz) Zittel, p. 204.
1890. *Eugnathus latus* (Egerton) Woodward & Sherborn, p. 78.
1895*b*. *Heterolepidotus latus* Egerton : Woodward, p. 304.
1924. *Heterolepidotus* ex. aff. *latus* Egerton : Rüger, p. 731, text-figs. 6, 7.
1939. *Heterolepidotus latus* Egerton : Brough, p. 76, figs. 34–39.

DIAGNOSIS. A *Heterolepidotus* of large size, attaining a length of 70 cm. Length of the head about a quarter of the total length of the fish, but shorter than the maximum depth of the trunk. The external skull bones are not extensively ornamented. The orbit is small and the scales serrated posteriorly. The total length of the fish is only three and a half times the greatest depth of the body. The dorsal fin is opposite to the pelvic fins with its posterior border immediately opposite the anterior border of the anal fin, which it much exceeds in size. The lepidotrichia are stout and numerous, and except in the caudal fin have no articulation over the proximal half of their length. They bifurcate distally and are formed of many small segments. Fulcra are small, but present on all the fins. Tail is hemiheterocercal, not deeply forked.

HOLOTYPE. *Heterolepidotus rhombifer* (Agassiz) a young individual of the species, B.M.N.H. P 3620 from the Lower Lias, Lyme Regis. The original type of *Semionotus rhombifer* Agassiz (1836).

MATERIAL. Specimens in the B.M.N.H. and Geological Survey Museum.

REMARKS. In his synonymy of *Heterolepidotus latus* Woodward (1895*b* : 304) includes *Dapedium fimbriatum* described by Agassiz (1834 : Feuill. 9 and 35 : **2**, pt. 1, p. 196). The specimen of *D. fimbriatum* came from Häring in the Tyrol, and is probably Triassic in age, and most certainly not Liassic since there are no outcrops of the latter in that area. The original which was in the Munich Museum was destroyed in the war, and consequently was not accessible to the present author. However, from the description and plate given by Agassiz, together with the locality (i.e. not Liassic), it is obvious that *Dapedium fimbriatum* is not synonymous with *Heterolepidotus latus* Egerton and must be removed as a separate species. Further "*Heterolepidotus*" *fimbriatus* (Agassiz) is not synonymous with the other Triassic species from that area, *Heterolepidotus striatus* (Agassiz).

In 1836 Agassiz described and figured *Semionotus rhombifer* from the Lower Lias of Lyme Regis and since this is synonymous with *Heterolepidotus latus* Egerton, but was described far earlier, then it must take priority over Egerton's species. The specific name is thus *Heterolepidotus rhombifer* (Agassiz).

Description. *Neurocranium.* No complete description of the structure of the neurocranium of this genus has so far been produced. The following description is drawn chiefly from specimen No. 60123 in the Geological Survey Museum, which consists of a dorso-ventrally flattened neurocranium, with the parasphenoid and vomers complete. The specimen comes from the Lower Lias of Lyme Regis.

Although it is considerably crushed, almost all the individual bone sutures and nerve foramina could be detected after treatment of the surface with formic acid. Posteriorly the basioccipital forms the notochordal pit, but no sutures can be seen in that region to indicate the demarcation between the lateral occipitals and the basioccipitals. As in *Caturus* (Rayner, 1948, fig. 3) there is no supraoccipital, the epiotics protruding from under the parietals to form a dorsally rounded region to the back of the neurocranium (Text-fig. 28). To either side of the epiotics lie the dermopterotics. These form the roof of an extensive temporal groove, in which the anterior extremities of the trunk muscles had their insertion during life. A similar temporal groove is found in the Teleosts. Beneath the epiotics are the lateral occipitals. These form a large portion of the hind wall, and at the same time border the foramen magnum. The intercalars are beautifully preserved and in hind view form a lower boundary to the temporal groove.

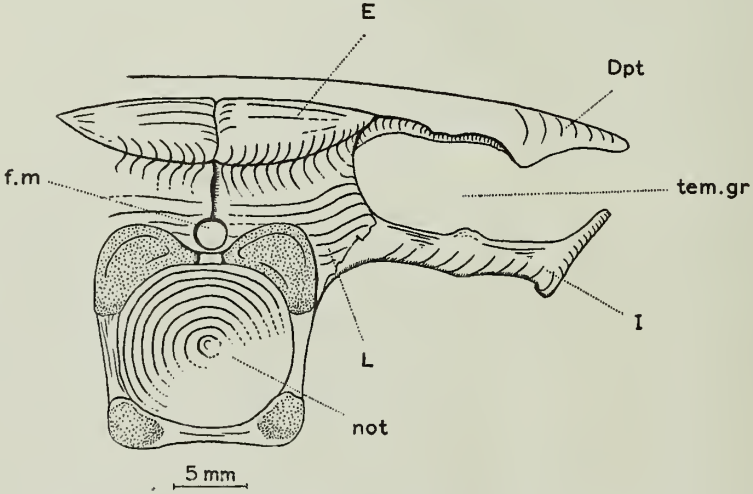

Fig. 28. *Heterolepidotus rhombifer* (Agassiz). Reconstruction of the neurocranium in hind view.

The lateral wall of the skull although completely flattened dorso-ventrally is still sufficiently undisturbed as to leave all the constituent bones in their relevant positions (Text-fig. 29). The intercalar is the most distinctive ossification and forms a large extent of the lateral wall. It is roughly triradiate in appearance, and is clearly distinguished by radiating fibres which stretch forward and downwards as in *Caturus*. Between the two more anteriorly directed processes of the intercalar is a distinct notch through which the vagal nerve was transmitted. The intercalar forms the upper, posterior and anterior margins of the vagal foramen, whilst the lower border is made up by an extension of the basioccipital. Anterior to the vagal foramen and a little above it, but still within the intercalar, the glossopharyngeal nerve had its exit. Anterior again to the intercalar is a somewhat fragmented prootic. Because of this fragmentation the origin of the seventh nerve and the

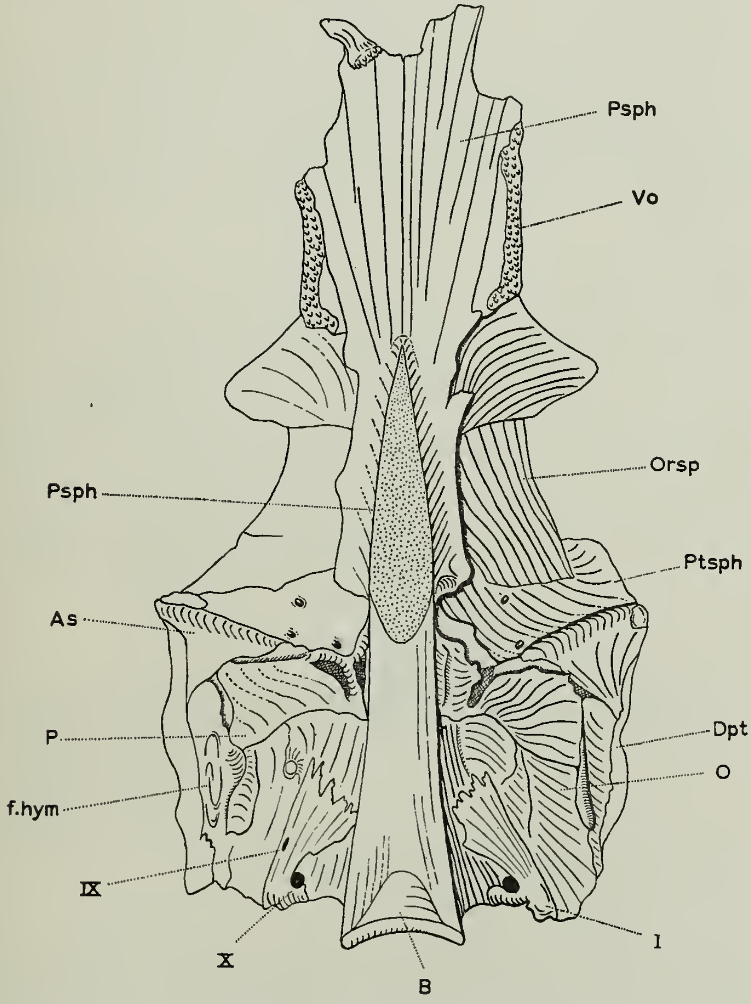

Fig. 29. *Heterolepidotus rhombifer* (Agassiz). Neurocranium in ventral view, slightly diagrammatic. From G.S. 60123.

subsequent passages of its component branches can be clearly traced (Text-fig. 30). The root of the seventh nerve goes back down through the prootic via a large foramen, posterior in position to the orbital surface. The hyomandibular branch of the seventh passes backwards and outwards on to the surface of the prootic, its passage being marked by a distinct groove. The buccal branch passes forwards and upwards and out on to the orbital surface via a small facial foramen. Through this facial foramen the jugular vein must also have been transmitted. The palatine branch of the seventh had a different course, passing forwards and downwards under a small bridge of prootic bone and out into the floor of the myodome. Ventral to the origin of the seventh nerve and running well beneath the surface of the prootic is a pronounced channel along which one of the branches of the internal carotid artery probably passed.

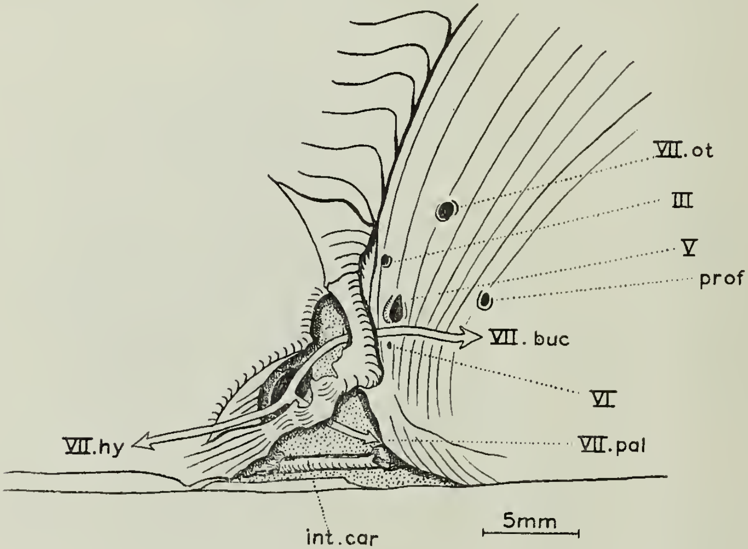

FIG. 30. *Heterolepidotus rhombifer* (Agassiz). Lateral view of neurocranium to show exits of the facial nerve. From G.S. 60123.

In the posterior otic region there appears to be another ossification. This bone fills in that region of the lateral wall from the prootic back to the intercalar. In my opinion it is obviously a quite separate ossification from that of the prootic and the intercalar, and must be termed an opisthotic. This conclusion is reached after examining all the three bones, which show lines of growth only compatible with three individual centres of ossification. The importance of the opisthotic in the Furidae will be dealt with in this discussion. Dorsally the opisthotic bears the hyomandibular facet, but the facet terminates anteriorly before it meets the autosphenotic. The autosphenotic is a large stout bone with a pronounced post-orbital process.

The orbital surface has been pushed forwards in fossilization, and ventrally has suffered from crushing. As a result it is difficult to deduce the size and depth of the myodome, but it was probably small as in *Caturus*.

The bony intraorbital septum appears complete, with the pterosphenoid and orbitosphenoid regions completely smooth. Immediately in front of the facial foramen is a large oval foramen which transmitted the trigeminal nerve. Ventrally to this is a much smaller foramen which probably served for the exit of the seventh cranial nerve. Dorsally to it are two more foramina, the first, the smaller of the two transmitted the third cranial nerve, whilst the second transmitted the otic branch of the facial nerve. Passing inwards towards the optic foramen is one more recognizable foramen which in life might have served for the passage of the profundus.

The parasphenoid is an elongated bone with a posterior smooth portion behind the orbits, and with a longer toothed portion in front. The teeth are small, granular and rounded, and form a dense series on the bone surface. Posteriorly this toothed area finishes in a gentle curve, but anteriorly in a distinct point. The bone continues forwards in front of this toothed region to form a smooth shelf beneath the vomers. Posteriorly it is bifurcated where it abuts the basioccipital. There is an appearance of a pair of small basipterygoid processes (Brough, 1939 : 81), but I can see no trace of an ascending process.

The structure of the vomers in this specimen appears different from that described by Brough (1939 : 81) from specimen B.M.N.H. P 7564, there being a narrow elongated area of vomer on either side of the parasphenoid bearing somewhat larger teeth than those found on the parasphenoid.

For a full description of the remainder of the fish see Brough (1939 : 76).

Genus ***CATURUS*** Agassiz, 1834

1833. *Uraeus* Agassiz, **2**, pt. 1, p. 12 (*non* Wagler, 1830).
1844. *Conodus* Agassiz, **2**, pt. 2, p. 105 (name only).
1851. *Strobilodus* Wagner, p. 75.
1858. *Endactis* Egerton, no. 4.
1866*a*. *Thlattodus* Owen, p. 55.
1866*b*. *Ditaxiodus* Owen, p. 107, pls. 4, 5.

DIAGNOSIS. Trunk long and fusiform. Pectoral fins large, exceeding the pelvics in size. Dorsal fin in advance of the anal, both triangular. The dorsal fin arises opposite or immediately behind the pelvics. Caudal fin hemiheterocercal and deeply forked. External skull bones and opercular apparatus only feebly ornamented with small tubercles and striae of enamel. Dentition : teeth on both the upper and lower jaws large and arranged in a sparse series. Teeth on the palatine and splenial smaller, those on the other palatal bones minute and granular. Maxilla long and straight sometimes slightly arched. Opercular deep, broader below than above. Subopercular smaller but of moderate size. Squamation : scales deeply overlapping and as broad as deep, feebly ornamented in part by tubercles and weakly crimped. Snout somewhat pointed and the cheek plates thin.

TYPE SPECIES. *Caturus furcatus* Agassiz.

Caturus chirotes (Agassiz)

(Text-figs. 31–36)

1836. *Eugnathus chirotes* Egerton, p. 368 (name only).
1842. *Eugnathus chirotes* Agassiz, **2**, pt. 2, p. 102, pl. 57*b*.
1844. *Conodus ferox* Agassiz, **2**, pt. 2, p. 105 (name only).
1890. *Eugnathus* (?) *chirotes* Agassiz: Woodward & Sherborn, p. 77.
1895*b*. *Caturus* (*Conodus*) *chirotes* (Agassiz) Woodward, p. 344, pl. 7, figs. 2, 3.

DIAGNOSIS. See Woodward, 1895*b* : 344.

HOLOTYPE. Imperfect fish, B.M.N.H. P 3643 from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the Geological Survey Museum Nos. 489 and 60124, both from the Lower Lias, Lyme Regis.

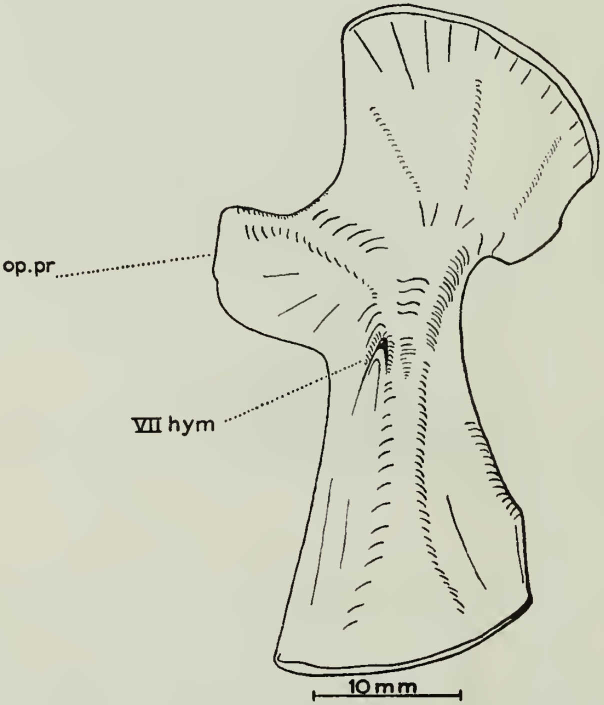

FIG. 31. *Caturus chirotes* (Agassiz). Right hyomandibular, external view. From G.S. 489*a*.

DESCRIPTION. The genus has been adequately described by Woodward (1895*b* : 344) and Rayner (1941, 1948 : 288). The following is in the form of a series of notes to supplement these accounts.

Hyoid arch. The hyomandibular is a stoutish bone in a nearly vertical position (G.S. 489*a*). It has a thickened, distinctly rounded head which articulates with the neurocranium by a deep articulatory facet in the prootic. The opercular process is well developed and lies at right angles to the main axis of the bone. A thickened strengthening ridge runs down from the opercular process to the base of the hyomandibular (Text-fig. 31). The foramen for the hyomandibular nerve is near the centre of the bone, just dorsal to the junction of the lower edge of the opercular process. The distal end of the hyomandibular is not quite so rounded as its head, but it is again strengthened for articulation with the symplectic and epihyal.

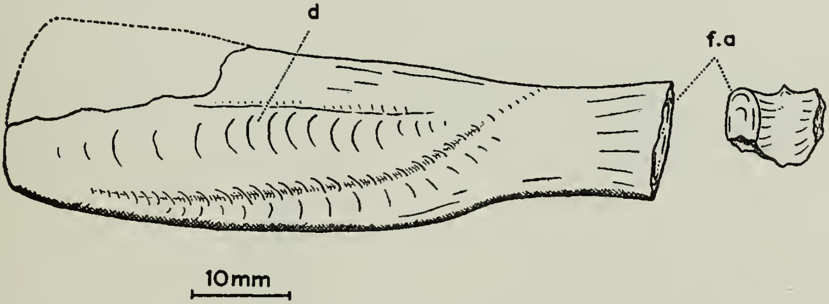

FIG. 32. *Caturus chirotes* (Agassiz). Ceratohyal and hypohyal of the left side. From G.S. 60124*b*.

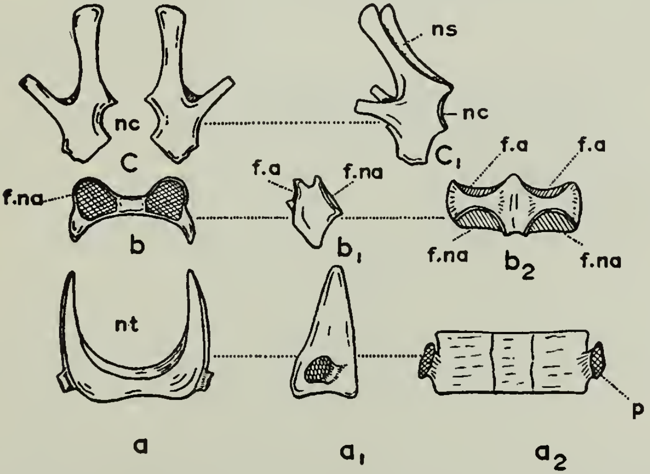

FIG. 33. *Caturus chirotes* (Agassiz). Caudal vertebra ; *a*, a_1, a_2 hypocentrum ; *b*, b_1, b_2 pleurocentrum ; *c*, c_1, neural arch. From G.S. 60124*c*.

A fragment of the epihyal remains between the hyomandibular and the ceratohyal in G.S. 60124, and this suggests that the epihyal was of comparatively small size.

In contrast the ceratohyal is a stout ossification, much thickened ventrally (Text-fig. 32). A distinct groove runs along it, first forwards and then upwards, disappearing before reaching the anterior end of the bone. Here the bone is considerably thickened, with a well-marked articular surface for the hypohyal.

Of the hypohyal only the dorsal half remains in G.S. 60124*b*. However, from the size of its articulatory facet it must have been a stout bone.

Vertebrae. The vertebrae of *Caturus* show a very primitive condition (Zittel, 1887 : 228). In this species each segment of the whole body shows two ossifications, an anterior pleurocentrum and a posterior hypocentrum, which together embrace the notochordal space. The pleurocentra bear articular facets for the neural arches which are wedged between them. In the caudal region the neural arches are divided into distinct halves, there being not only a cleft neural spine as in *Caturus furcatus*, but a complete division through the arch. The hypocentra have pronounced parapophyses in the trunk region for the articulation of the ribs. In the tail they bear haemal arches.

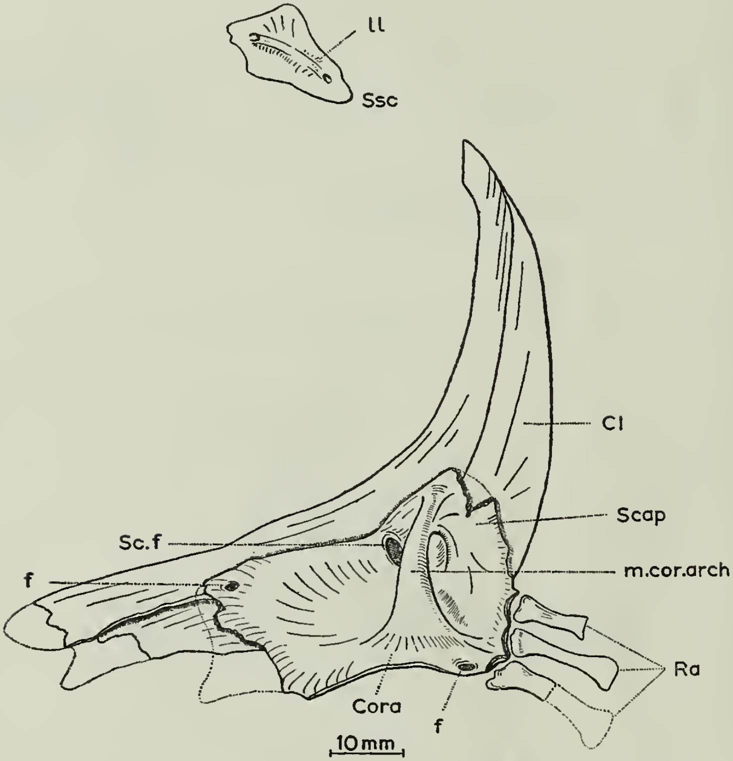

FIG. 34. *Caturus chirotes* (Agassiz). Internal view of right cleithrum and pectoral girdle. From G.S. 60124*d*.

Pectoral girdle. This has been extracted almost in its entirety from G.S. 60124*d* (Text-fig. 34). The suprascapular is a small bone which articulates with the skull in the region of the epiotics. Passing through the suprascapular is a branch of the sensory canal system which joins anteriorly with that from the extrascapular. Although the supracleithrum and postcleithrum are lost in this specimen, I have examined them on other specimens. The supracleithrum is considerably elongated and broadens somewhat ventrally. From its most ventral extremity it bears a narrow prolongation, which fits under the cleithrum. The sensory canal passes obliquely across it out on to the body scales. The postcleithrum is smaller than the supracleithrum and elliptical in general shape.

The cleithrum is a much curved bone with its anterior edge considerably thickened. The primary portion of the pectoral girdle is not cartilaginous as in the modern Holosteans *Amia* and *Lepidosteus*, but is completely ossified. The scapulo-coracoid is roughly rectangular in outline, the longer edge abutting against the cleithrum ; posteriorly it projects beyond the cleithrum and bears the glenoid surface, with which the three radials of the pectoral fin articulate (a similar condition is described by Rayner (1937 : 66) in *Leptolepis coryphaenoides*). Dorsally the scapular region has in it a large scapular foramen. On its inner surface the scapulo-coracoid bears a stout mesocoracoid arch, posterior to this foramen. The mesocoracoid arch is much more delicate in *Leptolepis coryphaenoides* (Rayner, 1937 : 66). In the lower Teleosts generally, it is very narrow while in the higher Teleosts it is absent (Boulenger, 1904*a* : 167). The ventral base of the mesocoracoid arch is pierced by the posterior diazonal nerve. There is no foramen for the anterior diazonal nerve and this must have passed in front of the mesocoracoid arch. One other small foramen is present, well forward in the coracoid region.

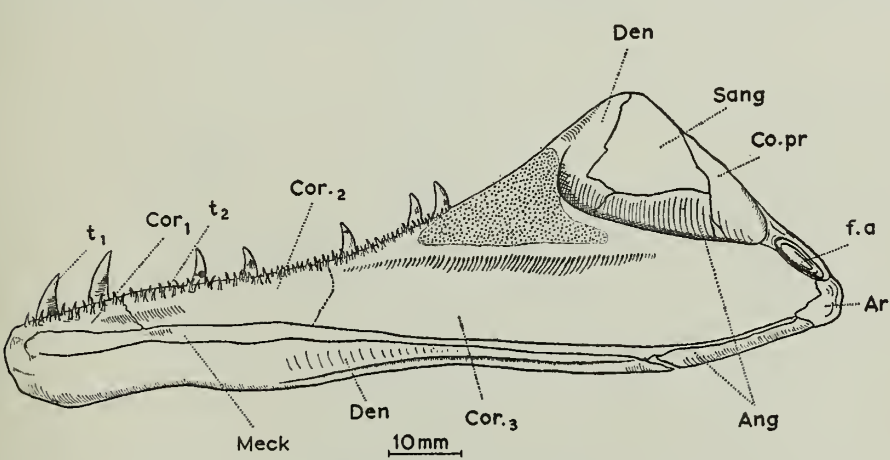

FIG. 35. *Caturus chirotes* (Agassiz). Inner view of right lower jaw. From G.S. 60124*e*.

The fin itself consists of twenty to twenty-five dermal rays inserted into a very short scaly lobe.

Lower jaw. Rayner (1948 : 291) has already partially described the lower jaw of *Caturus porteri* from an isolated mandible B.M.N.H. P 967. This description can usefully be supplemented by a further account of a complete lower jaw which

I have removed from a specimen of *Caturus chirotes* (G.S. 60124*e*).

The jaw consists of a dentary, angular, surangular, articular, coronoids and an ossified mento-Meckelian and shows a close resemblance to that of *Amia calva* (Text-fig. 35).

The dentary bears between ten and twenty large curved teeth, the anterior of which curves backwards, whilst the more posterior ones point forwards. There are at least two coronoids and probably three. If in fact there are these three separate coronoids, then the resemblance to *Amia* is striking. These bones make up most of the inner surfaces of the jaw, and dorsally bear numerous teeth. Dorsally on the most posterior coronoid (III) is a roughly triangular area covered in minute teeth.

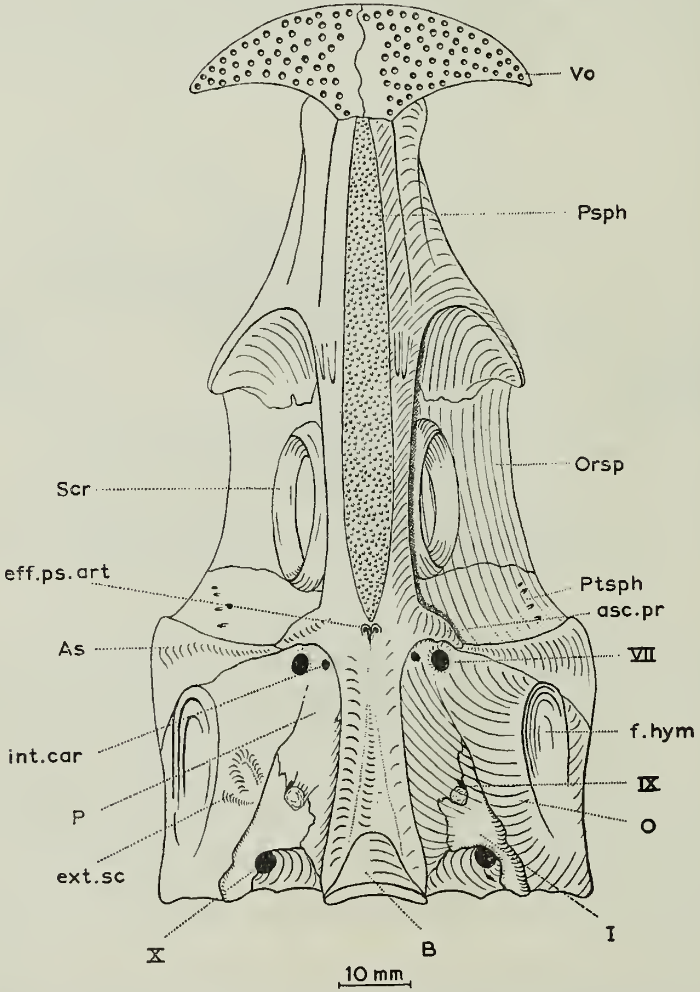

FIG. 36. *Caturus chirotes* (Agassiz). Neurocranium in ventral view. Right side somewhat restored. From G.S. 60124*f*.

From this point these bones bear teeth along their dorsal margins. These slender, sharply-pointed teeth are smaller than those borne by the dentary and far more numerous. The Meckelian bone is completely ossified, in contrast to the condition found in *Amia* and *Lepidosteus*. Posteriorly it forms the articular region which bears the articular fossa for the quadrate. Continuing upwards it forms an ossified coronoid process, which borders the angular and part of the surangular. The angular forms a large portion of the posterior quarter of the jaw. Above it are the triangular surangulars. All the suture lines in this region are well marked and easily discerned.

A large gular plate is found between the mandibles.

Skull and neurocranium. At first sight there seems little to add to what Woodward (1897 : 293) and Rayner (1948 : 289) have already said on the skull of *Caturus*. However, neither of these authors mentions a sclerotic ring in this genus, although in *Caturus chirotes*, two perfectly preserved sclerotic rings have appeared during acid treatment of G.S. 60124*f*. Text-fig. 36 shows a ventral view of the neurocranium, and from it several structures omitted by Rayner (1948) can be seen.

The parasphenoid is an elongate bone, with its anterior two-thirds covered by small sharp teeth. These are confined to an area near the centre of the bone as can be seen from Text-fig. 36. The ascending process passes backwards and upwards to meet the autosphenotic. In the mid-line in the region of the ascending process are two small foramina. These served for the passage of the efferent pseudobranchial arteries up into the parasphenoid. The transverse commissure between these two vessels, which exists in some Teleosts and which is recorded by Watson (1925 : 837) in the " Kansas Palaeoniscid " from the Coal Measures, could have existed since they are so close together, but there is no direct evidence of this. Anteriorly, the parasphenoid meets the paired vomers. Each vomer is much curved, almost sickle-shaped, and covered with long slender teeth. This contrasts with a statement by Woodward (1895*b* : 330) in which he maintains that the vomers in the genus *Caturus* bear teeth only at their anterior edges. The parasphenoid near its posterior extremity bifurcates to accommodate the basioccipital. Running down the centre of the parasphenoid posteriorly is a well-marked groove, which widens and deepens as it passes backwards. Finally, in the lateral wall of the neurocranium, above the intercalar and between it and the lateral occipital, is a further ossification. This is quite distinct and is clearly an opisthotic.

Family SEMIONOTIDAE

DIAGNOSIS. See Woodward, 1895*b* : 49.

Genus ***DAPEDIUM*** Leach, 1822

1833. *Tetragonolepis* Agassiz, **2**, pt. 1, pp. 6, 181 (in part).
1836. *Amblyurus* Agassiz, **2**, pt. 1, p. 220.
1845*b*. *Aechmodus* Egerton, p. 367.
1873. *Omalopleurus* Costa, p. 59, pl. 5, fig. 2*a*, *b*, *c*.

DIAGNOSIS. See Woodward, 1895*b* : 128.

TYPE SPECIES. *Dapedium politum* Leach.

Remarks. Most of the members of the genus *Dapedium* come from the English Lower Lias (particularly Lyme Regis). A few come from the Lower Lias of Alsace-Lorraine, and the remainder from the Upper Lias of Germany and France.

Dapedium sp.

(Text-figs. 37–41)

Material. A small isolated neurocranium from the Lower Lias of Stonebarrow, Charmouth. *Prodactylioceras davoei* zone, Green Ammonite Beds (Lower Limestone, Bed 123a). The specimen is in the B.M.N.H., registered Number P 11189.

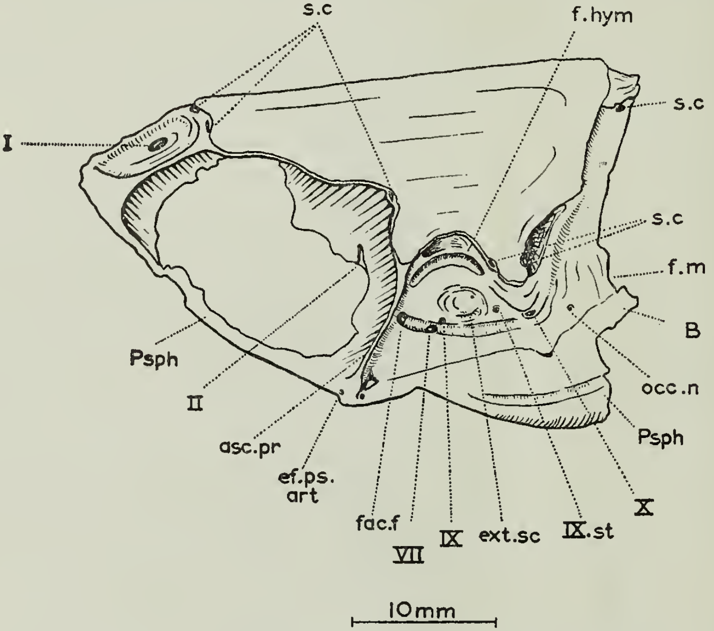

Fig. 37. *Dapedium* sp. Neurocranium in lateral view. From B.M.N.H. P 11189.

Description. *Neurocranium.* Only four specimens containing neurocrania are known of this genus. All of them have been previously described. The earliest description was published by Woodward (1893 : 563) consisting of a brief note on specimen B.M.N.H. P 3541. A few years later Frost (1913 : 219) gave a more extended description of specimen B.M.N.H. P 11177, and finally in 1948 Rayner published her paper on Holostean neurocrania, based on the other two specimens. One of these came from the Bath Museum (M.1280) and the other from the British Museum (Natural History) No. P 11189.

A re-examination of these four specimens showed that the two described by Woodward and Frost were so poorly preserved as to be useless for the determination of formina and suture lines. The third British Museum specimen (B.M.N.H. P 11189) seemed suitable for acid development. This was done and gave a complete neurocranium free from all surrounding matrix. Since both sides of the specimen are now visible, confirmation of existing foramina can be obtained by comparing one side with the other.

The skull of *Dapedium* is much more solidly constructed than that of its close relative *Lepidotes*, the ossification being complete (Text-fig. 37). The neurocranium is roofed by a continuous plate of membrane bone which has been formed by the fusion of the parietals, frontal and dermopterotic. This plate almost covers the entire brain-case, apart from a narrow flange which projects from behind this covering. There are no unossified areas in the neurocranium itself. Fusion of the individual bones is almost complete and suture lines are consequently not easy to recognize.

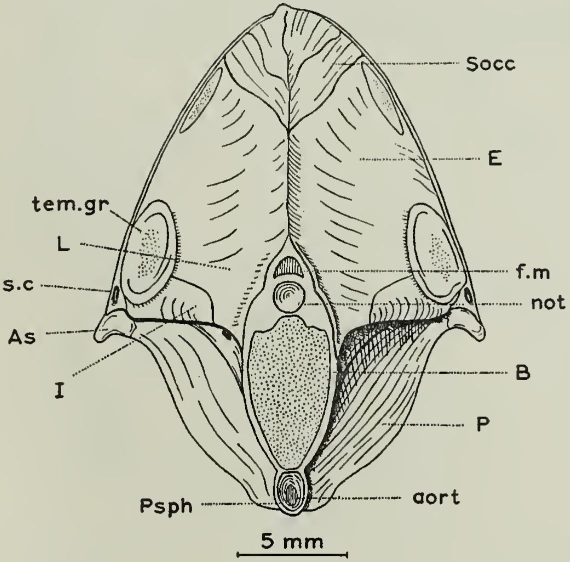

FIG. 38. *Dapedium* sp. Neurocranium, hind view, right side somewhat restored. From B.M.N.H. P 11189.

The postorbital portion of the neurocranium is the most difficult to interpret. However I agree with Woodward (1893, pl. 1, figs. 3 to 3*b*) and Frost (1913, fig. 2) that there is a well-defined supraoccipital forming the backwardly directed flange, and I cannot accept Rayner's suggestion that this is simply the two outstanding mesial edges of the epiotics (Text-fig. 38). The supraoccipital has a pronounced median crest projecting backwards for some distance. The epiotics and lateral occipitals make up the rest of the neurocranium in the postorbital region, but there is no distinct suture line separating them. The lateral occipitals form the border of the foramen magnum, and abut the intercalars ventrally. The demarcation of the intercalar is more pronounced and the true extent of this bone can be seen (Text-fig. 38). Just dorsal to the intercalars occur the temporal grooves. The lateral occipital continues round beneath the intercalars on to the lateral wall of the skull. In this region the tenth nerve emerged, the foramen for its exit being relatively large and directed backwards. Behind the tenth and nearer the foramen magnum is another small foramen which served for the exit of the occipital nerve (spinal nerve 1).

The basioccipital borders the notochordal pit, but it is the parasphenoid which forms the border of the ventral canal through which the dorsal aorta ran.

The major portion of the lateral wall of the neurocranium is made up of the prootic, which also covers the otic capsule (Text-fig. 39). In its dorsal region the prootic bears the hyomandibular facet, whilst just below this the position of the semicircular canals can be seen. Three clearly recognizable foramina are to be found in the prootic. The hindermost ones are for the exit of the ninth nerve. Of these two foramina the more posterior, smaller one transmitted the supratemporal branch of the ninth nerve, while the somewhat larger more anterior foramen transmitted the other branch. The two exits are separated by the external semicircular canals.

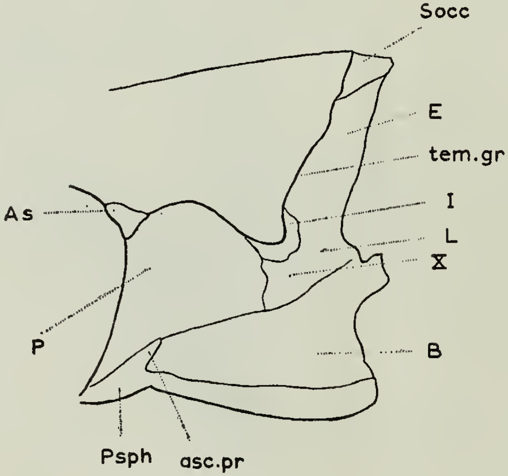

FIG. 39. *Dapedium* sp. Neurocranium, lateral view, slightly diagrammatic. After B.M.N.H. P 11189.

Again slightly to the anterior and just below the exit of the foremost branch of the ninth is a much larger foramen which served for the passage of the seventh nerve. The hyomandibular branch of the seventh must have passed straight down from this foramen into the hyomandibular bone, whilst the facial branch continued on and passed through the facial foramen into the orbit. There was no true trigemino-facial chamber, and in this respect *Dapedium* resembles its near relative *Lepidotes*.

The facial foramen is fairly large, and besides transmitting the buccal branch of the seventh it served for the passage of the jugular vein (Text-figs. 40 and 41). Running back from the facial foramen is a well-marked groove which continues across the surface of the prootic and the lateral occipital and was most probably for the reception of the jugular vein.

The autosphenotic is small in this species and again the suture line on the optic surface is indistinguishable. There is a small somewhat rounded basipterygoid process.

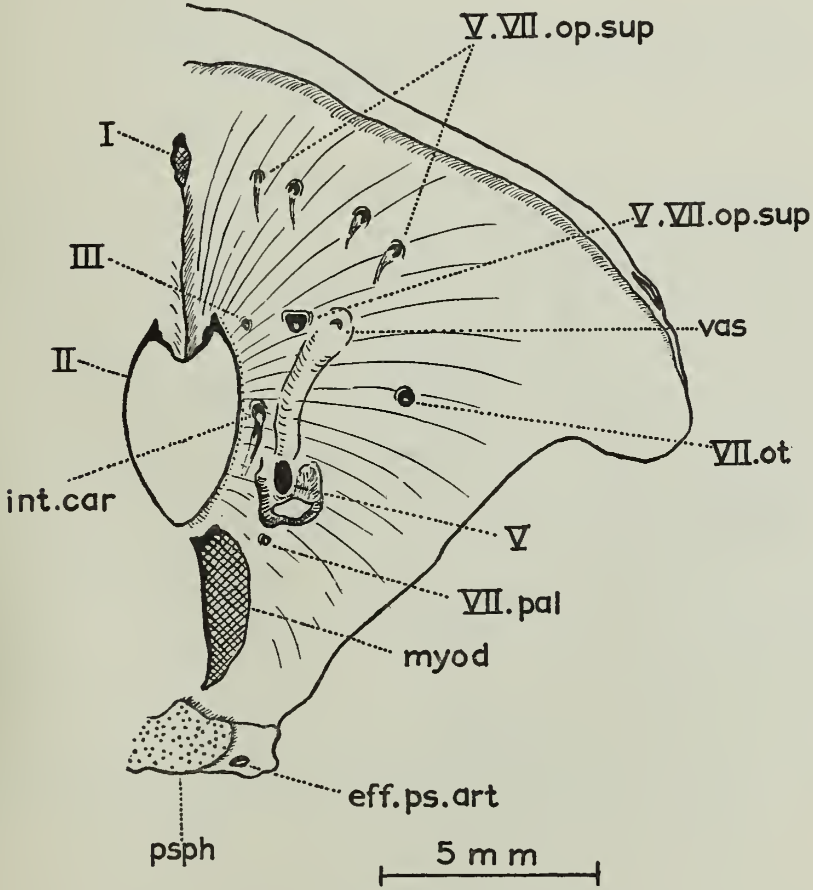

FIG. 40. *Dapedium* sp. Neurocranium as if cut vertically just anterior to the optic foramen, showing the left orbital surface. From B.M.N.H. P 11189.

The walls of the orbit, as pointed out by Rayner (1948 : 307) are not unlike those of *Lepidotes* and the infraorbital fenestra is fairly small. However, the fusion of the individual bones within the orbit is so complete that the demarcation of the pterosphenoid, autosphenoid and prootic cannot be seen. The basisphenoid is broken so that only a little of it remains, but the extent of the myodome on either side can still be made out.

All the foramina in the orbital surface are well defined and clearly recognizable. Immediately above the facial foramen, and partially let back into the roof of it so that it appears in a recess, is a larger foramen. From this issued the main branches (mandibular and maxillary) of the trigeminus. From the facial recess a groove ascends, finishing in a downwardly directed foramen. This appears to be vascular and served for the passage of a branch of the jugular vein into the neurocranium itself. Close to the side of this and towards the mid-line, is a larger foramen through which the superficial ophthalmic had its exit. Nearer to the mid-line again is a somewhat reduced opening which probably transmitted nerve III.

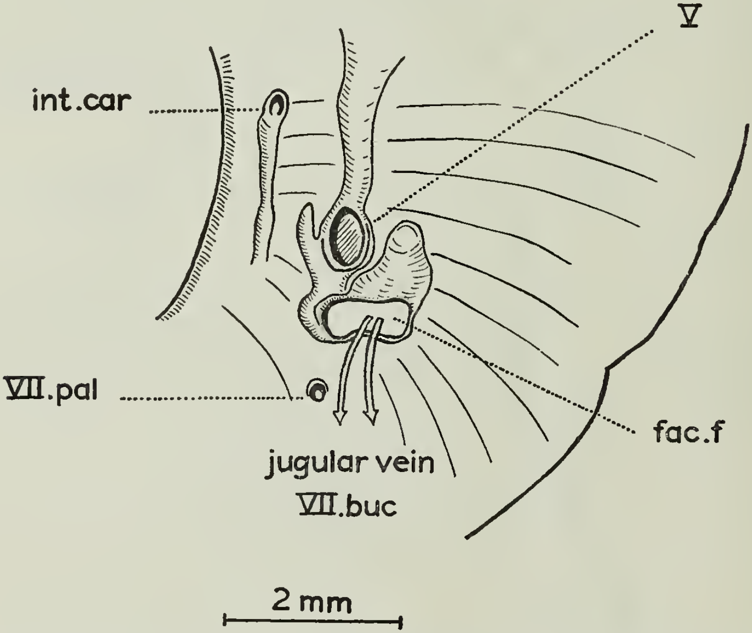

FIG. 41. *Dapedium* sp. Neurocranium as if cut vertically just anterior to the optic foramen, showing the basal portion of the left orbital surface. From B.M.N.H. P 11189.

Towards the roof of the orbit several foramina with downwardly directed grooves pierce the pterosphenoid. These were for secondary branches of the superficial ophthalmics, supplying sensory organs of the supraorbital canal.

The palatine branch of the seventh appears to have emerged through the small foramen which pierces the wall of the orbit just below the facial foramen, whilst a slit-like opening beneath nerve III probably transmitted the internal carotid artery.

The remaining foramen is more laterally situated than the rest, and from it the otic nerve emerged.

The two deep nasal pits are floored by the ethmoid and the posterior walls are pierced by a pair of foramina, through which the olfactory nerves ran. The parasphenoid in specimen No. 36705 from the Sedgwick Museum, Cambridge, bears a basipterygoid process ; at the base of this in specimen B.M.N.H. P 11189 is a small foramen which probably accommodated the efferent pseudobranchial artery.

An adequate description of the semicircular canal system has already been given by Rayner (1948 : 308).

Genus ***TETRAGONOLEPIS*** Bronn, 1830

1852. *Pleurolepis* Quenstedt, p. 214.
1860. *Homoeolepis* Wagner, p. 92.

DIAGNOSIS. Trunk laterally compressed, deeply fusiform or cycloidal with the abdominal region protuberant ventrally. Head small in relation to body and the interopercular is deeper than the subopercular. Teeth styliform with a conical apex, those on the dentary forming a regular series, longer than those on the maxilla. Suborbitals three in number and there is a complete circlet of nine orbitals bordering the orbit. Cleithrum sigmoidal in outline, quite unlike the cleithrum in the allied genus *Dapedium.* There are only three branchiostegal rays and these are characteristically arranged, the first having an unusual shape, both the anterior and posterior edges being concave. The vertebral column consists of distinct pleuro- and hypocentra, and the neural spines are always fused with their supporting arches. Both the neural and haemal spines in the caudal region bear a laminar expansion at the base of their anterior borders. The paired fins are small and delicate, the pectorals arising at the level of the subopercular and the pelvics arising on the posterior edge of the protuberance. The dorsal fin is elongated as in *Dapedium* arising about the middle of the back, with the anal fin shorter and opposed to the hinder end of the dorsal. The caudal fin is not forked. All the lepidotrichia are distally segmented and bifurcated. The scales are quadrangular, very deep on the ventral portion of the body, but less deepened above the lateral line. Scales are smooth or feebly tuberculated with a much thickened anterior border which forms the peg-and-socket articulation. The ventral ridge scales are much larger than the dorsal, but both are serrated.

TYPE SPECIES. *Tetragonolepis semicincta* Bronn.

Tetragonolepis discus Egerton

(Text-figs. 42, 43)

1853. *Tetragonolepis discus* Egerton, p. 278, pl. 11, fig. 5.
1860. *Pleurolepis discus* (Egerton) Wagner, p. 96.
1895*b*. *Tetragonolepis discus* Egerton : Woodward, p. 160.

DIAGNOSIS. A Tetragonolepid almost cycloidal in outline and with a less protuberant abdominal region. It is smaller than the type species and the scales are smooth apart from a series of concentric growth lines. The posterior margin of the scales is entire and not serrated.

LECTOHOLOTYPE. B.M.N.H. P 7625, the type nominated by Woodward (1895*b* : 160), from the Upper Lias, Gloucestershire.

MATERIAL. Specimens in the B.M.N.H. and the Royal Scottish Museum, Edinburgh.

DESCRIPTION. *The skull.* The skull roofing bones are feebly ornamented. The greatest degree of ornamentation is found on the suborbitals, which are covered by numerous tubercles of enamel. That on the extrascapulars, parietals and frontals is sparse, confined to a few isolated tubercles. The remaining skull bones appear smooth, in particular those constituting the opercular apparatus.

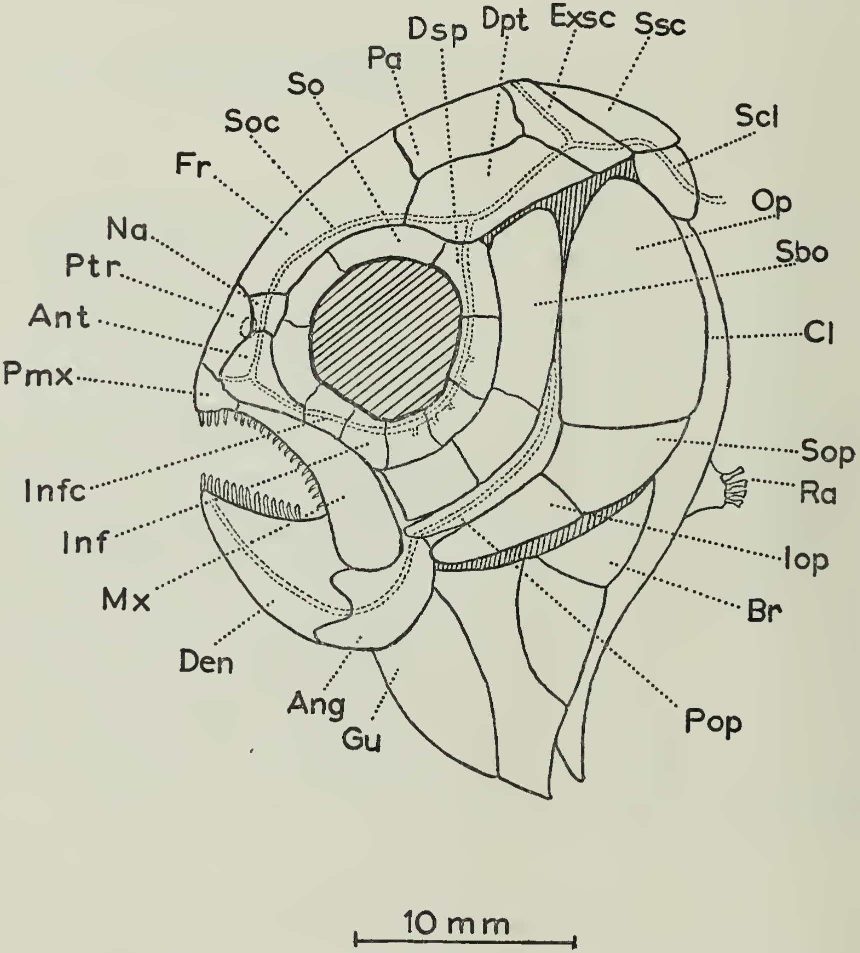

FIG. 42. *Tetragonolepis discus* Egerton. Restoration of skull in lateral view.

The skull roofing bones are invariably fused to one another making the suture lines difficult to decipher. The parietals are almost square in outline, bounded on either side by the larger dermopterotics (Text-fig. 42). The extrascapular is of the usual shape in contrast with the arrangement seen in *Dapedium* where a series of four or more bones occur in the corresponding position. Behind the extrascapular is the large suprascapular, to which the pectoral girdle articulates. Anteriorly the broad frontals abut the postrostral and the nasals. The whole region of the snout is difficult to interpret, and in order to appreciate the individual bones and their relationship it was necessary to supplement the material of *T. disca* by an examination of the allied species *T. semicincta.* The postrostral is larger than the nasal, spatulate in shape dorsally and narrowing as it runs forwards. The nasal is small and quadrangular, in contact with the postrostral anteriorly and the antorbital ventrally. The antorbital is triangular, articulating with the postrostral and premaxilla anteriorly and the maxilla ventrally. Whether or not external nares were present in this area could not be ascertained with certainty. The nasal, postrostral and antorbital are all discernible on one specimen of *T. semicincta,* R.S.M. 1877–30.3, while B.M.N.H. P 3625 of the same species displays the antorbital. Further, on B.M.N.H. P 1595 (*T. semicincta*) a postrostral element is apparent. The premaxilla is small and short, bearing some three or four teeth along its lateral edge (R.S.M. 1901–70.3, *T. discus*). The maxilla is longer and stouter with a spatulate expansion posteriorly. No trace of a supramaxilla was observed. The teeth on the maxilla are similar to those on the premaxilla and dentary but are somewhat smaller and do not continue right to the posterior end of the bone.

A complete ring of orbital plates surrounds the eye, nine in number including the dermosphenotic. Between the posterior infraorbitals and the opercular apparatus lie three suborbital bones. The most dorsal one is by far the largest and runs almost the full length of the opercular. The opercular is much larger than the subopercular and the whole apparatus forms an arched series.

Lower jaw. The lower jaw is almost identical with that of *Dapedium* and includes a dentary, angulo-articular and a toothed prearticular. The dentary bears only a marginal tooth row and the suture line between it and the angulo-articular follows a zig-zag course as in *Dapedium.*

Between the rami of the lower jaws is a large gular plate, this is followed by a series of three branchiostegal rays. The first branchiostegal ray has concave anterior and posterior edges, and behind it fit two further rays more triangular in shape. Both the gular plate and the rays are almost smooth with no noticeable tuberculations (B.M.N.H. P 7623).

Palate. The parasphenoid is narrow and does not appear to bear teeth. The quadrate is small articulating with a larger metapterygoid. The major portion of the palate is made up of the very deep ento- and ectopterygoids, together forming an extensive but thin sheet, stretching from the hinder end of the maxilla to the parasphenoid (R.S.M. 1901·70.3). The inner surfaces of these pterygoids are smooth and not dentigerous.

Hyoid arch. On no specimen of *T. discus* was this recognizable. However, on one specimen of *T. semicincta* (R.S.M. 1879·30.3), a ceratohyal is present. It is a stout ossification, narrow posteriorly but expanding considerably towards its anterior extremity.

Sensory canal system. The main cephalic division of the sensory canal runs through the ventral edge of the extrascapular, giving off the supratemporal commissure. It continues through the dermopterotic, dermosphenotic and round the infraorbital series as the infraorbital canal. Anteriorly it enters the antorbital where it divides, one half continuing forwards, presumably into the postrostral, while the other unites with the supraorbital canal in the nasal. The supraorbital canal passes upwards through the frontals and unites with the infraorbital canal in the dermopterotic. The preopercular canal is prominent, and passes into the lower jaw as the mandibular canal.

Appendicular skeleton. A small supracleithrum articulates the suprascapular to the cleithrum. The cleithrum itself continues downwards to almost the ventral border of the body. Ventrally the cleithrum curves backwards, giving the girdle an unmistakable sigmoidal flexure, not met with in *Dapedium.* At the level of the subopercular the ossified primary girdle supports four radials (B.M.N.H. P 3624). The fin is delicate and made up of approximately twelve lepidotrichia.

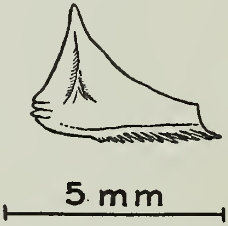

FIG. 43. *Tetragonolepis discus* Egerton. Ventral ridge scale. From B.M.N.H. P3624.

The pelvic girdle consists of two small bony rods articulating some seven or eight delicate lepidotrichia. The fin arises near the bottom of the ventral protuberance of the body, in a corresponding position to that in *Dapedium.*

Unpaired fins. The dorsal fin stretches from the dorsal apex of the body almost to the tail, and like the somewhat shorter anal fin has the same number of endoskeletal supports as lepidotrichia. The caudal fin is not forked and in *T. semicincta* has eight haemal spines supporting the lower lobe (R.S.M. 1901·70.2).

Axial skeleton. The vertebral column consists of distinct pleuro- and hypocentra. The neural spines are fused to the supporting arches, and in the anterior portion of the body, that is in front of the dorsal fin, extend to the body margin. The haemal spines are shorter and do not reach the ventral border, but both these and the neural spines in the posterior region bear a small laminar expansion at the base of their anterior borders. There are no intermuscular bones.

Squamation. The scales, unlike that condition seen in *Dapedium,* have a sharply thickened rib on the inner face of their anterior borders. This forms the peg-and-socket articulation. The scales are quadrangular in shape and very deep on the ventral portion of the body, there being only five scales between the ventral margin and the lateral line. Above the lateral line there are some eight or ten scales, these are much smaller and nothing like as deep. Both the dorsal and ventral ridge scales are delicately serrated (Text-fig. 43).

Genus *LEPIDOTES* Agassiz, 1832

DIAGNOSIS. See Woodward, 1895*b* : 77 ; 1916 : 26.

TYPE SPECIES. *Lepidotes elvensis* (Blainville).

Lepidotes mantelli Agassiz

(Text-figs. 44, 45, 47)

1826. Figures of marginal teeth, Webster, pl. 6, figs. 5, 6.
1827. Scales, Mantell, p. 58, pl. 5, figs. 3, 4, 15, 16.
1833. (?) *Lepidotus subdenticulatus* Agassiz, **2**, pt. 1, p. 9, pl. 30, figs. 4–6.
1833. *Lepidotus mantelli* Agassiz, **2**, pt. 1, p. 9, pl. 30, figs. 10–15 ; pl. 30*c*, figs. 1–7.
1835. *Lepidotus fittoni* Agassiz, **2**, pt. 1, p. 265, pls. 30*a*, 30*b*.
1836. *Tetragonolepis mastodonteus* Agassiz, **2**, pt. 1, p. 216, pl. 23*e*, figs. 3, 4.
1841. *Lepidotus mantelli* Agassiz : Owen, p. 69, pl. 30, fig. 1 ; pl. 31.
1849. *Lepidotus mantelli* Agassiz : Williamson, p. 444.
1854. *Aechmodus mastodonteus* (Agassiz) Morris, p. 317.
1854. *Lepidotus fittoni* Agassiz : Morris, p. 331.
1854. *Lepidotus mantelli* Agassiz : Morris, p. 332.
1860. *Lepidotus fittoni* Agassiz : Lee, p. 458, pl. 12.
1887. *Lepidotus mantelli* Agassiz : Branco, p. 345, pl. 3, figs. 1, 2.
1890. *Lepidotus mantelli* Agassiz : Woodward & Sherborn, p. 112.
1895*b*. *Lepidotus mantelli* Agassiz : Woodward, p. 108, text-figs. 23, 24.
1896. *Lepidotus mantelli* Agassiz : Scupin, p. 162, pl. 9, fig. 8..
1908. *Lepidotus mantelli* Agassiz : Lankester, p. 79, text-fig. 46.
1916. *Lepidotus mantelli* Agassiz : Woodward, p. 36, pl. 7, fig. 7 ; pl. 8, figs. 1–4 ; pl. 9 ; pl. 10, figs. 1–3 ; text-figs. 16–18.

DIAGNOSIS. See Woodward, 1895*b* : 109 ; 1916 : 36.

LECTOTYPE. B.M.(N.H.) 2456 from the Wealden, Heathfield, Sussex, nominated as the type by Woodward (1895*b* : 109).

MATERIAL. Specimens in the Leicester Museum and Brit. Mus. (N.H.), from the Wealden of Sussex.

REMARKS. The neurocranium of this genus has received much previous attention. Woodward first described that of *Lepidotes latifrons* (1893 : 560) and later that of *Lepidotes mantelli* and another species of *Lepidotes* (1916, pl. 10, text-figs. 15, 16). More recently Holmgren & Stensiö (1936, fig. 364) described the neurocranium of *Lepidotes semiserratus*, and the same species is dealt with by Rayner (1948 : 305). Beltan (1957) described a neurocranium of the genus *Lepidotes* from the Bathonian of Morocco, which he assigns to the species *L. mantelli*. Apart from the fact that his specimen comes from the Lower Jurassic and that the earliest members recorded for *L. mantelli* are Wealden, the ossification of the neurocranium is very incomplete and in this respect it resembles *Lepidotes semiserratus* far more closely than it does *L. mantelli*. However, I found in the Leicester Museum a complete neurocranium and associated palate of *Lepidotes mantelli* from the Hastings Sands, Tilgate (Leicester Museum No. O.S. 5′ 1957), which after preparation has yielded sufficient information to make a redescription necessary.

Further, two isolated prootics of *Lepidotes latifrons* (B.M.N.H. P 9998) from the Oxford Clay at Peterborough have been cleaned up in acid, and confirmation of all the existing foramina in the prootic of *Lepidotes mantelli* obtained.

DESCRIPTION. *Neurocranium.* This is well ossified. All the bones constituting the neurocranium are stout and cancerous, together forming a much more solid and heavy brain-case than in *Lepidotes semiserratus* (Rayner, 1948 : 305). The large prootics which have grown back over the lateral and basioccipitals have eliminated most of the cartilaginous interspaces seen in earlier species.

The epiotics are large and meet in the mid-line. Posteriorly they present a triangular appearance forming over half of the depth of the occiput, and there is no supraoccipital. Beneath the epiotics lie the even larger lateral occipitals which, meeting in the mid-line, extend ventrally to form the upper rim of the foramen magnum. The lateral occipitals extend a considerable distance on to the lateral wall of the neurocranium, completely surrounding the foramen for the vagal nerve (Text-fig. 44). Dorsally abutting on the lateral occipital and not quite reaching the anterior edge of the epiotic is a small intercalar (opisthotic of Woodward, 1916, pl. 10, fig. 1).

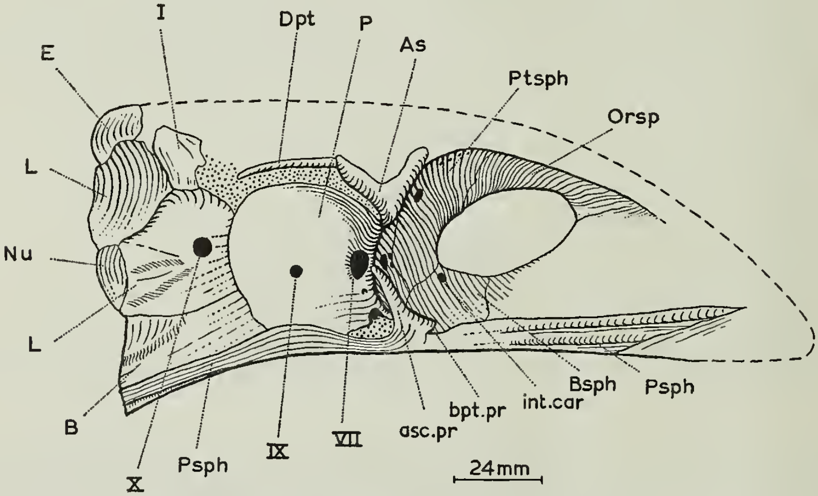

FIG. 44. *Lepidotes mantelli* Agassiz. Neurocranium in lateral view, slightly diagrammatic. From Leicester Museum O.S. 5, 1957.

Beneath the lateral occipital is a massive basioccipital which is capped posteriorly by a pair of neural arches. The basioccipital is distinctly grooved below for the basicranial canal.

The prootic is another large element which posteriorly meets both the basioccipital and the lateral occipital, but which is separated from the intercalar by a cartilaginous interspace. Dorsally there is a narrow unossified space between the prootic and the dermopterotic. The hyomandibular has its articulatory facet up on the underside of the projecting dermopterotic. The lateral wall of the prootic is pierced by the glossopharyngeal and facial foramina. The antero-ventral corner of the prootic is unossified and there is a distinct notch marking the entry of the internal carotid artery. The bones of the orbital surface are distinct and the foramina obvious (Text-figs. 44–46).

The myodome is small but the basisphenoid is of the same massive proportion as in *Lepidotes semiserratus* (Rayner, 1948, fig. 12). A downwardly directed foramen near the upper margin of the basisphenoid was clearly for the entry of the internal carotid.

There is a distinct gap between the ascending process of the parasphenoid and the edge of the prootic (not shown in Text-fig. 45) and it is probable that it served for the passage of the jugular vein into the orbit (see Text-fig. 44).

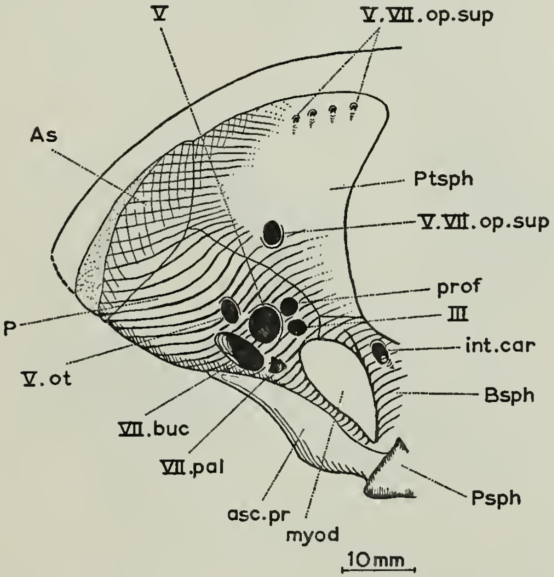

Fig. 45. *Lepidotes mantelli* Agassiz. Neurocranium as if cut vertically just anterior to the optic foramen, showing the right orbital surface. From Leicester Museum O.S. 5, 1957.

The facial foramen is set back in the bone and the passages of its various components can be clearly demonstrated in the isolated prootic of *Lepidotes latifrons* (B.M.N.H. P 9998). The hyomandibular branch passes back out on to the lateral wall of the prootic, whilst the largest foramen opening into the orbital surface transmitted the buccal branch of the facial. Immediately below this foramen is a much smaller and downwardly directed foramen through which passed the palatine branch. Dorsally to the facial foramen and nearer the mid-line is another large somewhat recessed foramen which served for the exit of the trigeminus. Above and between the facial and trigeminal foramina is a smaller foramen for the otic branch of the facial. Nearer the mid-line again from the trigeminal foramen and still within the boundary of the prootic are two further foramina, the more dorsal transmitted the profundus, while the larger ventral one served for the passage of the occulomotor nerve. The remaining recognizable foramen in the prootic is small and occurs in the groove beneath the foramen of the palatine branch of the facial. It probably transmitted the abducens nerve during life (Text-fig. 46).

The pterosphenoid has an upwardly directed foramen next to its lower boundary that marks the exit of both the superficial ophthalmic nerves; several passages piercing the upper region of the same bone are for the secondary branches inervating the supraorbital canal. The bony infraorbital septum is perforated by an infraorbital fenestra with which the optic foramen is confluent. In the ethmoidal region the olfactory nerves are invested in bone, the true homologues of which are uncertain.

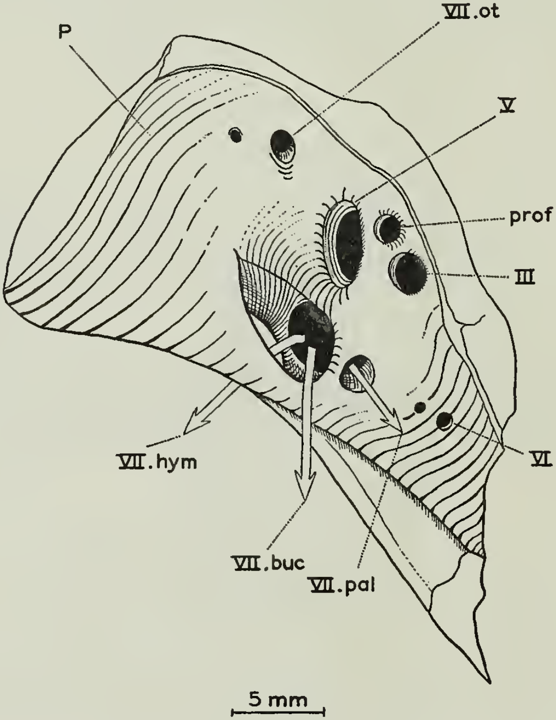

Fig. 46. *Lepidotes latifrons* Woodward. Right prootic viewed from the orbital surface. From B.M.N.H. P 9998.

The parasphenoid curves sharply downwards posteriorly and the distinction between the ascending and basipterygoid processes is slight. There is no rounded notch in front of the basipterygoid process as described by Rayner (1948 : 306) in *Lepidotes latrifrons*.

The neurocranium of *L. mantelli* is very similar in make up to that of the related Semionotid, *Dapedium* (p. 300). In *Dapedium* the same number of bones form the lateral wall of the neurocranium and the relationships of the nerve foramina to the bones are essentially the same. The foramen for the exit of the hyomandibular and buccal components of the seventh nerve is situated in the lateral wall posterior to the orbit in both *Dapedium* and *Lepidotes*. Two important differences are the presence of an aortic canal in *Dapedium*, absent in *Lepidotes*, and the presence in *Dapedium* of a bone filling the posterior-dorsal angle in the back of the skull, which I have termed the supraoccipital although it is probable that this bone is not homologous with the supraoccipital of other Holosteans. Both forms have a small intercalar and an extensive lateral occipital and in neither is there an opisthotic present.

Palate. The palate of *Lepidotes semiserratus* has been described by Rayner (1948, fig. 10). However, that of *Lepidotes mantelli* differs in a few respects sufficient to warrant a description (Text-fig. 47).

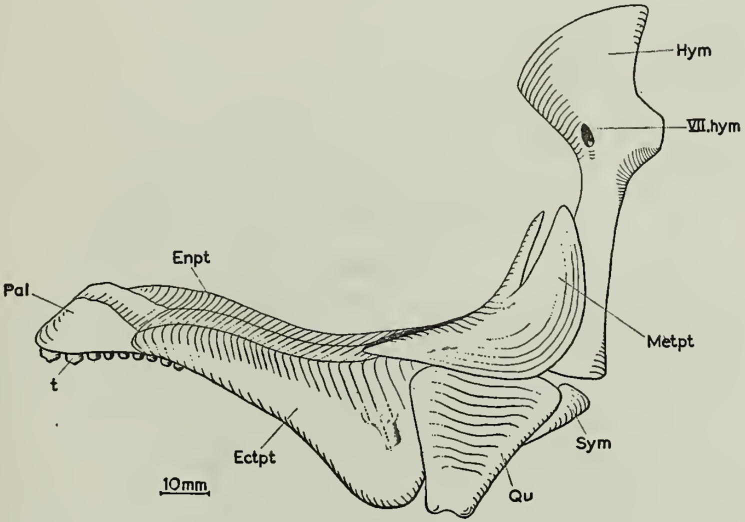

FIG. 47. *Lepidotes mantelli* Agassiz. Reconstruction of the left palate. From Leicester Museum O.S. 5, 1957.

The mandibular suspensorium is only slightly inclined forward and the hyomandibular is stout with a posterior projection for the support of the opercular bone. The metapterygoid is an extensive ovoid-shaped bone with a V-shaped notch in its posterior border. This bone is distinctly flattened in a horizontal plane, but curves sharply upwards posteriorly. Its inner edge articulates for a short distance with the basipterygoid process and it is probable that the outermost posterior flange fitted over the ventral portion of the hyomandibular. The quadrate is stout and there is a small symplectic between it and the hyomandibular. The ectopterygoid is the largest bone in the palate and forms with the entopterygoid a broad ledge running out from the parasphenoid in a more or less horizontal plane. The ectopterygoid then turns downwards almost through a right angle to constitute the outer edge of the palate. The entopterygoid itself is a narrow strip of bone filling the gap between the parasphenoid and the ectopterygoid. Woodward (1916, fig. 16) figures a transverse section of the palate of *Lepidotes mantelli* and from this the extent of the entopterygoid and ectopterygoid can be seen. Anteriorly the ectopterygoid bears teeth and in front of it and often fused indistinguishably with it is the stout tooth-bearing palatine. Between the palatines and pterygoids of either side is a large vomer, also bearing teeth.

Family LEPTOLEPIDAE

DIAGNOSIS. See Woodward, 1895*b* : 500.

Genus ***LEPTOLEPIS*** Agassiz, 1832

1839. *Ascalabos* von Münster, p. 112.
1848. *Tharsis* Giebel, p. 145.
1850. *Sarginites* Costa, p. 285.
1850. *Megastoma* Costa, p. 287.

DIAGNOSIS. See Woodward, 1895*b* : 501.

TYPE SPECIES. *Leptolepis coryphaenoides* (Bronn).

Leptolepis africana sp. nov.

(Text-fig. 48)

DIAGNOSIS. Much smaller than the type species not exceeding 5 cm. in length, of which the head and opercular apparatus constitute approximately 1·3 cm. The suture between the frontals is almost a straight line with nothing like the wavy nature seen in *Leptolepis coryphaenoides*. The supramaxillaries are appreciably deeper than the maxilla and together form a comparatively greater sheet of bone than in the type species. The ornamentation of the supramaxillaries is characteristic, consisting of diagonal wavy ridges of enamel running antero-dorsally, postero-ventrally, whilst the diagonal ridges of enamel on the maxilla run postero-dorsally, antero-ventrally. The scales are cycloidal, ornamented with concentric rings of enamel.

HOLOTYPE. B.M.N.H. P 38526 and counterpart P 38527 from the Trias? of Mandawa, Tanganyika.

MATERIAL. The unique holotype, comprising head and two-thirds of the body.

REMARKS. This is the first record of the genus *Leptolepis* occurring in East Africa. The earliest known members of this genus have generally been regarded as of Upper Liassic age. However, there is one specimen of *Leptolepis* of undoubted Triassic age known to the author, which is in Professor D. M. S. Watson's collection and this comes from Seefeld, Austria. The holotype here described was discovered in a boring put down by the B.P./Shell Petroleum Development Co. of Tanganyika Ltd. at Mandawa, Tanganyika, and generously presented by them to the Department of Palaeontology of the British Museum (Natural History). The co-ordinates of this Mandawa Well are: 9° 24′ 58″, 4 S. and 39° 25′ 3″, 7 E., and the specimen of *Leptolepis africana* was discovered at a depth of 10,520 ft. It seems possible that the age of the bed containing the holotype could be from Upper Triassic to Lower Liassic and it is hoped that accurate dating will be forthcoming in the near future.

DESCRIPTION. *The skull.* The external bones of the skull are covered by a very thin layer of enamel. The majority of the bones are smooth, but the maxilla and supramaxillaries exhibit a characteristic ornamentation. On the supramaxillaries the ornamentation takes the form of a few wavy ridges running antero-dorsally, postero-ventrally. On the maxilla the ridges are confined to the central position where they run in the reverse direction, viz. postero-dorsally, antero-ventrally.

The frontals are by far the largest bones of the skull roof, broad behind but narrowing sharply between the orbits. The suture line between these much elongated frontals is almost straight, and does not exhibit the sinuosity seen in the type species. Anteriorly the edges of the frontals are even narrower, being scalloped out for the reception of the nasal bone. Both the frontal and nasal bones abut on to the rostral. The rostral is a small ossification and forms the lower border of the nasal orifice, the nasal itself forming the upper boundary. There is some evidence of a further bone between the nasal and the orbit, and it is reasonable to suppose that there was an antorbital present in that position. The parietals are small and square with a larger dermopterotic making up the remainder of the lateral border of the skull roof. Behind the parietal is the extrascapular and a much enlarged suprascapular. The suprascapular is relatively larger than that seen in *Leptolepis*

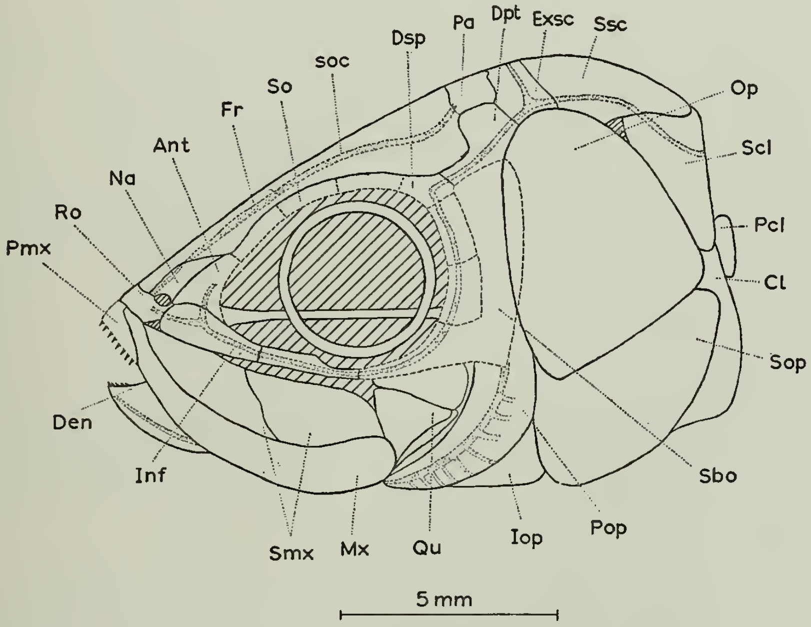

FIG. 48. *Leptolepis africana* sp. nov. Restoration of skull in lateral view.

coryphaenoides and more reminiscent of the suprascapular in *Pholidophorus similis*. Of the supraorbital and infraorbital series of bones, little can be made out. Anteriorly, however, adjoining the antorbital and rostral bones above, and the anterior supramaxilla beneath, is a large spatulate-shaped ossification which is the most anterior member of the infraorbital series. It narrows somewhat posteriorly where it meets the next member of the infraorbital series. These two bones together form a bar beneath the orbit.

The maxilla is long and curved, deepening somewhat at its posterior extremity. The lower border of the maxilla is convex except at its anterior extremity where it becomes concave for the reception of the small premaxilla. Above the maxilla are two elongated supramaxillaries of approximately the same size. These overlap the maxilla to a certain extent. No teeth were recognizable on the maxilla.

Of the lower jaw little can be made out, but the opercular apparatus seems identical with that of *Leptolepis coryphaenoides*. The state of preservation is too poor to make out other structures such as a sclerotic ring, palate, etc.

Appendicular skeleton. The pectoral girdle is a stout ossification. The supracleithrum is a long blade-shaped bone, broadest dorsally and carrying the hindermost portion of the main lateral line canal. The cleithrum is much thickened ventrally, especially where it articulates with the primary portion of the pectoral girdle. The membrane bones of the primary girdle are ossified as in the later, Liassic species. A delicate postcleithrum is also present.

The pectoral fin consists of some sixteen to twenty lepidotrichia, which are not jointed proximally.

The pelvic girdle consists of two triangular-shaped bones, with thickened lateral borders. The insertion is narrow, there are no supporting radials and the innermost fin-ray has no enlarged basal portion for the articulation of neighbouring rays, as described by Rayner (1937 : 67) in *Leptolepis coryphaenoides*. Instead the base of the stoutest outermost fin-ray is curved inwards to function probably as support for at least the next two succeeding lepidotrichia.

The lepidotrichia of the pelvic fin number between thirteen and fifteen.

Unpaired fins. The dorsal fin arises at almost the same level as the pelvic fins, but the number of fin-rays present in both it and in the anal could not be counted accurately. Both are supported by radials. The caudal fin is missing from the specimen.

Axial skeleton. The vertebrae, ribs and intermuscular bones are all similar to that described by Rayner (1937 : 68) in *Leptolepis coryphaenoides*.

Squamation. The body is covered in cycloidal scales, all delicately ornamented with concentric rings of enamel.

SCALE STRUCTURE OF PHOLIDOPHORUS AND LEPTOLEPIS

The evolution of the Teleosts from the Pholidophorid-Leptolepid line has been demonstrated by Rayner (1934, 1938) and Saint-Seine (1949*a*) on gross structure.

One of the most marked characteristics of the Teleosts is the structure of their scales. The scales of typical Teleosts are cycloidal and composed of several thin layers of bone (lamellae). Within these bony layers there are no cells and no structures such as blood vessels or tubules of any description. This type of scale without enclosed cells is a highly specialized structure that must have evolved from the normal cell-bearing bone of the scale of more primitive Actinopterygians (Klaatsch, 1890; Reis, 1895; Stephan, 1900; Goodrich, 1913; Voigt, 1934; Ørvig, 1951, 1957; Bernhauser, 1954). According to Reis (1895 : 163) the more primitive Teleosts such as the Elopidae, Characinidae and Salmonidae possess a scale which, like that of their " Ganoid " ancestors, is rich in normal bone cells. In the more specialized Teleosts these cells have disappeared, not only from the scales, but from the dermal bones.

The typical " Palaeoniscid " scale (Williamson, 1894; Scupin, 1896; Goodrich, 1907, 1913; Stensiö, 1932; Gross, 1935, 1947; Aldinger, 1937; Ørvig, 1951, 1957) consists of three layers, an outermost layer of enamel, beneath it a layer of dentine and basally a thicker layer of bone. Entering the scale from the basal face and ascending towards the dentine layer are numerous canals of Williamson (Ørvig, 1951 : 362). These vascular canals connect with the dentinal tubules which form a close network just below the enamel. The dentinal tubules secrete the layer of dentine. Throughout the bony tissues are numerous cell spaces.

From the " Palaeoniscoid " type of scale develops the " Lepidosteoid " type (Goodrich, 1913 : 758) which is characteristic of the majority of Holostei. In the " Lepidosteoid " type of scale the dentine layer has disappeared together with the dential tubules, and the canals of Williamson although present have lost their contained blood vessels and become functionless. However, there are still numerous cell spaces throughout the bony tissue.

Ørvig (1957 : 487) has shown in certain Palaeonisciformes how the reduction of cells in the bony tissues could have come about. In the Subholostean *Perleidus stoschiensis* Stensiö from the Lower Lias of East Greenland, the bone cells have assumed a somewhat unequal distribution by the concentration of some of them near the canals of Williamson. A more advanced stage occurs in the Palaeoniscid *Scanilepis dubia* (Woodward) from the Rhaetic beds of Scania, where all the bone cells of the hard tissue have become concentrated in the vicinity of the canals of Williamson. Finally, in the Palaeoniscid *Orvikuina vardiaensis* Gross from the Baltic Upper Middle Devonian, the canals have lost their original vascular function and the bone cells have become withdrawn into their interior. This series is, of course, stratigraphically in reverse.

Pholidophorus higginsi Egerton (Text-fig. 49)

The genus *Pholidophorus* ranges from the Upper Trias to the Upper Jurassic (Purbeckian), *Pholidophorus higginsi* being one of the first species of the genus to appear. The specimen sectioned, B.M.N.H. 41279, came from the Rhaetic of Aust. The scales are thick, rhombic and deeply imbricating, with their hinder margins often somewhat rounded.

Microstructure. The structure of the scale can be seen from Text-fig. 49 and is similar to that type of scale termed " Lepidosteoid " by Goodrich (1907 : 758).

There is a thick outer layer of enamel (ganoine) on the surface with a much thicker bony layer beneath. The basal bone tissue contains large cell spaces, and is penetrated by numerous, fairly thick, canals of Williamson. These canals ascend more or less vertically from the basal face of the scale, terminating just below the enamel.

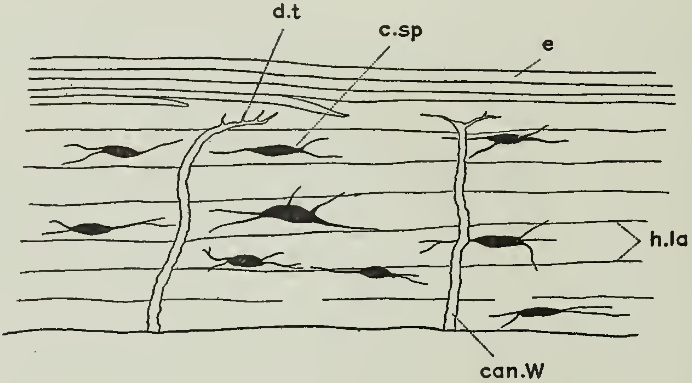

Fig. 49. *Pholidophorus higginsi* Egerton. Vertical section of scale. From B.M.N H. 41279, × 250 approx.

Pholidophorus caudalis Woodward (Text-fig. 50)

This second species of *Pholidophorus*, *P. caudalis*, was selected because it occurs later geologically, and has scales very different from those of the Rhaetic form. They are generally thinner, although still deeply imbricating. The specimen sectioned came from the Lower Lias of Lyme Regis, B.M.N.H. P 939*a*.

Microstructure. The scale is much thinner and the layer of enamel quite thin. The significant difference between this species and *P. higginsi* is the complete absence of recognizable cell spaces in *P. caudalis* (Text-fig. 50). The cells have already been withdrawn from the bone tissue. The canals of Williamson no longer appear vascular, and are very few in number. Whether or not these few remaining canals of Williamson contained the missing bone cells from the surrounding bone tissue could not be ascertained.

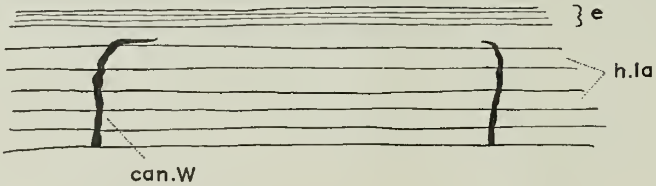

Fig. 50. *Pholidophorus caudalis* Woodward. Transverse section of scale. From B.M.N.H. P 939*a*, × 200 approx.

Leptolepis concentrica Egerton

The scales of this genus are no longer rhomboidal, but resemble more closely those of the Teleostei. They are cycloidal, very thin and with only a trace of a layer of enamel on them. They are also deeply imbricating. The specimen sectioned came from the Lower Lias of Lyme Regis, B.M.N.H. P 3666.

Microstructure. The surface is covered in an extremely thin layer of enamel, with a thin bony layer beneath. There are no cell spaces recognizable, and no canals of Williamson.

Comments. Thus, within the genus *Pholidophorus* the reduction in the cells of the bony layer can be observed. The Rhaetic species *P. higginsi* shows a normal distribution of cells, whilst the later Liassic species *P. caudalis*, shows an almost complete absence of them. Further, the canals of Williamson, which are no longer needed now that the dentine layer has disappeared, also show reduction within the genus ; *P. higginsi* has a plentiful supply, whereas in *P. caudalis* there are very few.

In *Leptolepis* these changes are carried further, with the complete disappearance of the canals of Williamson and also of the cells of the bony layer. Apart from the thin layer of enamel the scales of *Leptolepis* are perfectly normal Teleostean scales.

If we assume that the bony cells once lost cannot be re-acquired, as would be expected in view of the general, though not invariable, irreversibility of evolutionary process, then it is clear that the Elopidae, Cyprinoidea and Salmonidae must have separated off from the main Teleost stock at the *Pholidophorus* level of evolution and that *Leptolepis* cannot be ancestral to them.

Family Pycnodontidae

Diagnosis. Trunk much laterally compressed, discoidal or very deeply fusiform. External skull bones robust, with a median supraoccipital plate separating the parietals. Cheek bones very rarely present. Where they occur they are thin and delicate. Mandibular suspension inclined well forwards, gape small. Dentition : teeth prehensile on the premaxilla and dentary, and tritoral on the vomer and splenials. Opercular apparatus distinctive, with a small opercular and a much enlarged preopercular. Never more than a much reduced series of branchiostegal rays. No ossification in the notochordal sheath, lepidotrichia stout, well spaced and articulated. The lepidotrichia equal their supporting radials. Fulcra generally absent. Dorsal and anal fins extended and have long insertions. The scales are rhombic with well-marked peg-and-socket articulations. Squamation often confined to the anterior region. Tail hemiheterocercal.

Genus ***EOMESODON*** Woodward, 1918

DIAGNOSIS. Profile of head especially steep, and abdominal region of the trunk deepened. Caudal region relatively small. Not less than three outer series of splenial teeth.

TYPE SPECIES. *Eomesodon liassicus* (Egerton).

Eomesodon liassicus (Egerton)

(Text-figs. 51–54)

1854. *Pycnodus liassicus* Egerton, p. 436.
1855. *Pycnodus liassicus* Egerton : Egerton, no. 10, pl. 10.
1856. *Mesodon liassicus* (Egerton) Heckel, p. 202.
1895*b*. *Mesodon liassicus* (Egerton) : Woodward, p. 202.
1917. *Mesodon liassicus* (Egerton) : Woodward, p. 388.
1918. *Eomesodon liassicus* (Egerton) Woodward, p. 54, fig. 21.
1949*b*. *Eomesodon liassicus* (Egerton) : Saint-Seine, p. 334, fig. 1.

DIAGNOSIS. An *Eomesodon* with only one of the principal vomerine teeth coarsely crimped or tuberculated round the apex of the crown. Ornamentation of the skull roofing bones and the scales consists of closely arranged, large, flattened tubercles. In the caudal region each neural spine beneath the dorsal fin is double, and the number of lepidotrichia in the dorsal and anal fins less than in the typical *Mesodon*.

HOLOTYPE. Imperfect fish in the B.M.N.H. 19864, from the Lower Lias, Barrow-on-Soar, Leicestershire.

MATERIAL. Specimens in the B.M.N.H. and Worcester Museum.

REMARKS. This species was first described by Egerton (1854 : 436) and is known from only four specimens. Two of these are the part and counterpart of the same fossil, one half being in the British Museum, P 1336, and the other in the Worcester Museum. Woodward (1895*b* : 203) has given the locality for P 1336 as the Lower Lias, Tarn Hill, Tewkesbury, Gloucestershire. However, on checking this locality on the Ordnance Survey map, I find that he has misinterpreted the original label, and the true locality should be Sarn Hill, Bushley, Gloucestershire.

DESCRIPTION. In general profile the head of *Eomesodon liassicus* is very steep. The anterior region of the trunk is elevated dorsally and the abdominal region much deepened. The tail is smaller than in the genus *Mesodon* and the squamation is complete over the whole of the trunk in advance of the median fins.

The skull. The skull, with a small median supraoccipital, is very similar in pattern to that of the typical Pycnodonts (Text-fig. 51). The cranial roof is ornamented with regular longitudinal rows of tubercles, often with striation between the rows. On the preopercular and the opercular the rows of tubercles follow the length of the bone.

On each side of the median supraoccipital is a large parietal. This bone is roughly rectangular in shape but with a blunt point anteriorly, reaching to the border of the orbit. From the course of the sensory canals along the posterior border of this bone I think that this is a compound ossification incorporating the parietal and extrascapular (or the post-temporal of Traquair, 1879, pl. 4; White, 1932 : 82). The digitate prominence behind the parietal (X of Woodward, 1918, pl. 14, fig. 4) seen on many of the other Pycnodonts, possibly represents the vestiges of the suprascapular. This prominence has not been observed on any of the four specimens of this species, because the preservation in that area is poor. Beneath the parietal is a large dermopterotic (supratemporal—intertemporal of earlier workers) which borders the parietal ventrally. It is a deep four-sided plate tapering sharply forward above the orbit and forming part of its border. Posteriorly it has a long free border under which the supracleithrum lies. Beneath the dermopterotic is a much smaller rectangular plate separating it from the opercular and preopercular proper. This plate clearly belongs to the preopercular series since a continuation of the main preopercular canal runs through its anterior edge. In this respect *Eomesodon* resembles *Bobasatrania* and some of the Platysomids.

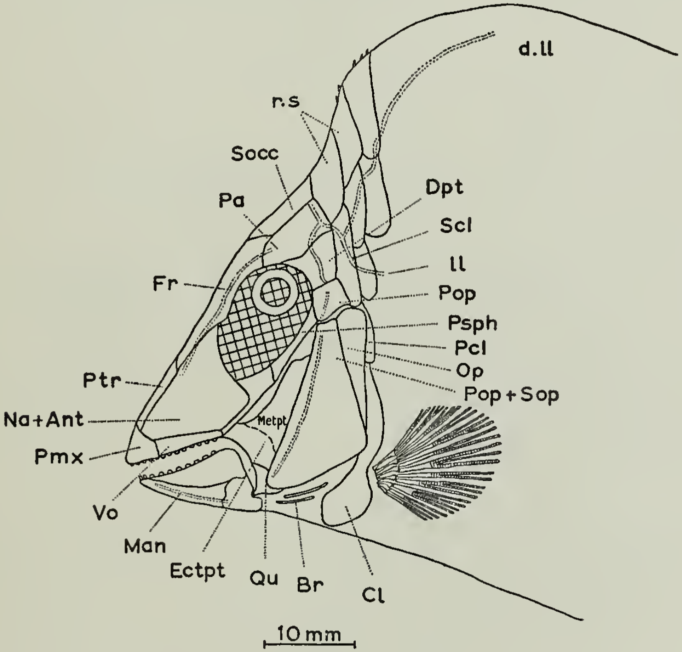

FIG. 51. *Eomesodon liassicus* (Egerton). Restoration of skull in lateral view.

The skull roof in front of the supraoccipital is composed of a pair of large frontals which are the largest bones of the skull. Traces of the sensory canal can be seen on them. They are expanded posteriorly, forming the antero-dorsal border of the orbits; and anteriorly they taper to meet another ossification which I have called the postrostral. Anteriorly the postrostral reaches the paired premaxillae. These are not complete on any of the specimens, but an impression of one can be seen on B.M.N.H. P 1336. The premaxilla is a small bone and it appears to have borne teeth. In front of the orbit there is only one large plate on either side, termed the mesethmoid by Woodward (1917 : 386). This so-called mesethmoid is a composite bone probably representing both the nasal and the antorbital. It is a stout thick bone, triangular in shape, and limits the orbit anteriorly. It is bounded below by the parasphenoid and the vomer. The supraorbital canal runs into the dorsal corner of the nasalo-antorbital, but its subsequent passage was not evident.

The parasphenoid extends forwards to the posterior corner of the nasalo-antorbital where it joins the single vomer. It is relatively stout anteriorly, but narrows beneath the orbit. The vomer is widened to support the stout dentition, and it projects beneath the ventral border of the nasalo-antorbital. The teeth on the vomer are mainly smooth with the principal tooth coarsely crimped or tuberculated round the apex of the crown (Egerton, 1854 : 436, B.M.N.H. 19864). There is evidence of an ossified sclerotic ring, but no cheek plates were observed. The preopercular is large and triangular with a much reduced opercular along its dorso-posterior border. The preopercular possibly represents a fusion of two bones, the preopercular and the subopercular.

The mandibular suspensorium is inclined forwards, with the ventral end of the hyomandibular in front of its dorsal end. Traces of the hyomandibular can be seen on B.M.N.H. P 1336 and there does not appear to be any anterior expansion to support the opercular. Ventrally there is a gap between the hyomandibular and the quadrate where the symplectic must have fitted. This is borne out by the presence of a distinct notch in that region of the quadrate. The quadrate is distinctly triangular with an articulatory surface ventrally ; this fits neatly into the corresponding facet in the angular of the lower jaw.

Lower jaw. The lower jaw is composed of three ossified elements only : the splenial, the dentary and the angular (Text-fig. 52). The splenial forms the greatest part of the mandibular ramus and bears most of the teeth, with the thinner dentary flanking it. The angular forms the posterior termination of the jaw, and the articulation with the quadrate. The splenial teeth are smooth and not indented, and there are not less than three outer series (cf. B.M.N.H. 35577). The dentary bears only two, somewhat chisel-shaped teeth with the outer one the larger. The teeth on the splenial are shorter and broader.

Beneath the preopercular are two fragments of bone which may represent the vestiges of the branchiostegal system.

Palate. The quadrate has a thickened posterior edge and dorsally articulates with the pterygoid arch. The pterygoid arch as far as can be judged consisted of two bones. Posteriorly the metapterygoid extends upwards to just below the parasphenoid and anteriorly the ectopterygoid forms a concave arch from the anterior edge of the quadrate to the vomer.

Sensory canal system. The sensory canal system of the head can quite easily be traced by the application of turpentine to the various bones. The supraorbital canal commences in the parietal and passes forward into the frontal. The bone preservation in that area is poor, and the canal can only be followed for a short distance. However, a further portion of the supraorbital canal can be traced in the postero-dorsal corner of the mesethmoid. Traces of the preopercular canal were found near the anterior border of that bone, and further evidence of it can be seen in the small separate preopercular plate above.

The infraorbital canal is continuous with the cephalic division of the main lateral line, and curves down through the dermopterotic. Its further passage is again obscured by the poor state of preservation in that area. The cephalic division of the main lateral line passes upwards on to the ventro-posterior margin of the parietal, where it gives off a well developed supratemporal commissure. The presence of this cross commissure on the hind margin of the parietal suggests that the parietal represents two bones, the parietal and the extrascapular. Posterior to the supratemporal commissure, the main lateral line turns downwards into the antero-dorsal corner of the supracleithrum passing diagonally backwards through this bone and then out on to the body scales as the main lateral line. The dorsal lateral line is a narrower canal, situated more superficially. It begins in the centre of the dorsal portion of the supracleithrum where it communicates with the main lateral line. It passes upwards and backwards to the dorsal edge of the supracleithrum, and then continues into the body scales, running along parallel with the dorsal margin of the body. It can be traced back almost to the dorsal fin.

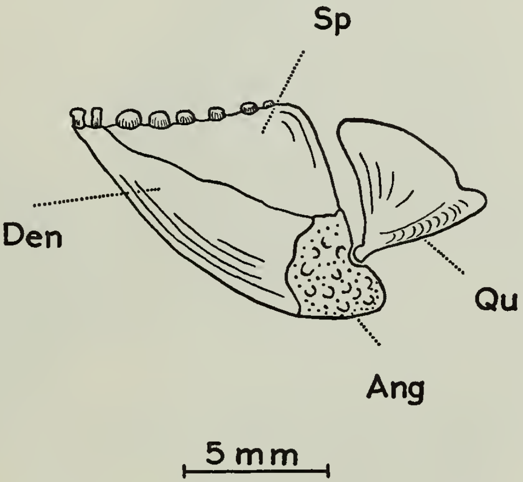

FIG. 52. *Eomesodon liassicus* (Egerton). Lower jaw and quadrate. From B.M.N.H. P 1336.

The main lateral line is well developed and its structure can be seen on B.M.N.H. P 5127. The canal appears to open to the surface between each scale, there being a distinct gap between the end of the canal on one scale and the recommencement of it on the succeeding scale. Anteriorly on each scale there is a fine ventral tubule which runs forwards and ends blindly (Text-fig. 53). The dorsal lateral line opens outwards by a small circular pit on the anterior border of each scale through which it passes.

Appendicular skeleton. The dermal bones of the shoulder girdle consist of a supracleithrum, a cleithrum and probably a postcleithrum. The anterior edge of the supracleithrum lies under the parietal and the dermopterotic. Between it and the cleithrum is another plate which could be an enlarged scale, but which is more probably the postcleithrum. The cleithrum itself is vertically elongated, tapering above and with a spatulate expansion beneath the opercular apparatus. The endoskeletal portion of the pectoral girdle has not been observed, and it was possibly only slightly ossified. The pectoral fin is attached just above the inferior expansion of the cleithrum. There is a single series of radials, six in number, all of which are somewhat expanded posteriorly. The lepidotrichia number about fifteen and are stout and segmented transversely. They dichotomize distally, but no fulcra have been observed along the anterior margin of the pectoral fin.

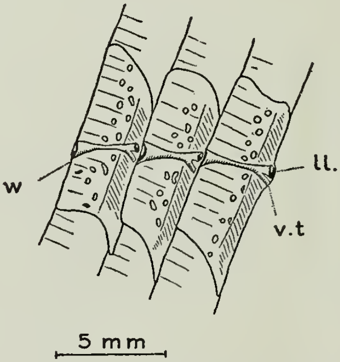

FIG. 53. *Eomesodon liassicus* (Egerton). Part of the squamation with a portion of the main lateral line. From B.M.N.H. P 5127.

The pelvic fins are not preserved on any of the specimens.

Unpaired fins. The lepidotrichia of the dorsal and anal fins are equal in number to their supports, which are more numerous than the neural spines in that region (Text-fig. 54). The number of lepidotrichia in the dorsal fin is about twenty-four, and these articulate with the rounded, expanded ends of the radials. The lepidotrichia bifurcate distally and are transversely segmented along their whole length. There are no traces of fulcra on either the dorsal or anal fins.

The anal fin is smaller than the dorsal with approximately fifteen lepidotrichia. Although these dichotomize distally, the transverse segmentation does not commence until the dichotomy begins.

The caudal fin has between eighteen and twenty lepidotrichia and its posterior margin is convex.

Axial skeleton. The notochord is persistent and the neural and haemal arches are well ossified. The neural and haemal spines of the vertebrae do not reach the dorsal border of the body, there being a set of radials interposed between the ends of the spines and the base of the fins. Neither the haemals nor the neurals bear laminar expansions in the caudal region. However, except near the tail the neural spines beneath the dorsal fin are double, each having a short slightly curved rod arising from the anterior portion of the neural arch, followed by the long backwardly directed neural spine proper.

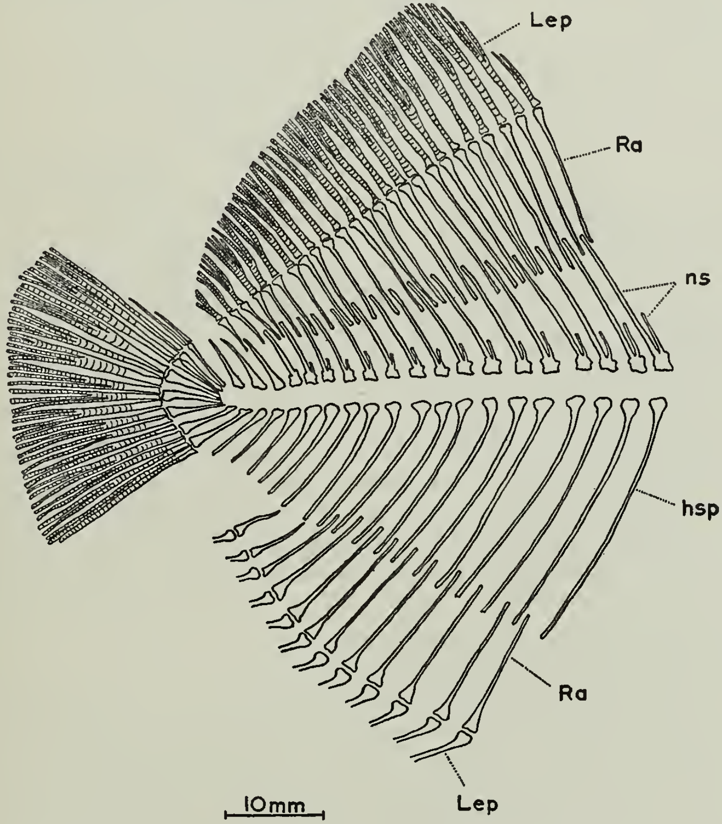

FIG. 54. *Eomesodon liassicus* (Egerton). Restoration of the endoskeleton of the trunk.

Squamation. The squamation is complete over the whole of the trunk in advance of the median fins. The scales are largest in the nuchal region and are ornamented with coarse tubercles, somewhat finer than those on the parietals and frontals.

The dorsal ridge scales are much deepened and modified ; the shape of the foremost ridge scales in the Worcester specimen being very different from that of the holotype. These dorsal ridge scales have the normal, median row of hooked denticles (4–6), those in front of the dorsal eminence being inclined backwards, those behind inclined forwards. The ventral ridge scales have no hooked or recurved denticles, but are more pointed just in front of the anal fin, somewhat resembling fulcral scales. Woodward (1918 : 56) gives the number of scales in a transverse series in the deepest part of the trunk as eight above the lateral line and ten below it. The majority of the scales are small, not much deepened and bear fewer tubercles than those in the nuchal region.

Order COELACANTHIFORMES

Family COELACANTHIDAE

DIAGNOSIS. See Woodward, 1891 : 394.

Genus *HOLOPHAGUS* Egerton, 1861

1834 *Undina* Münster, p. 539 (nomen nudum)
1842 *Coelacanthus* Münster, p. 57 (in part).

DIAGNOSIS. Trunk robust, dorsal fins well developed, supplementary caudal fin prominent. All the lepidotrichia are broad and stout, often expanded, and closely articulated in the distal portion. Small denticles are present on the preaxial rays of both the caudal and the first dorsal fins. External skull bones ornamented with tubercles and ridges of enamel. Plates of pelvic girdle distinctive (see Text-fig. 58). Basal plates of anal and second dorsal fins deeply bifurcated. Basal plate of first dorsal fin triangular. Dentition : teeth absent on jaw margins ; a few hollow conical teeth on the vomers and premaxillae.

TYPE SPECIES. *Holophagus striolaris* (Münster).

REMARKS. The genus *Holophagus* has previously been known as *Undina* and attributed to Münster (1834 : 539). However, as used by Münster it is a *nomen nudum* and as in the same year it was used by Gould (1834, pl. 383) in describing a genus of birds, it is no longer valid for use in fish nomenclature. The first valid generic name was that used by Egerton (1861) when he described *Holophagus gulo*.

Two species, *Holophagus gulo* and *Holophagus barroviensis*, have been recorded from the Lower Lias of this country. The descriptions of both are inadequate by modern standards. The species *H.* (?) *barroviensis* according to Woodward (1891 : 413) " is imperfectly definable ", and that material which has been assigned to this species is, in my estimation, for the most part of doubtful affinities. As a consequence, the only certain species of Coelacanth recorded from the Lower Lias of this country is *Holophagus gulo*, and it is to the description of this species which I shall mainly confine my remarks.

Holophagus gulo Egerton

(Pl. 42 ; Text-figs. 55–58)

1861. *Holophagus gulo* Egerton, p. 19.
1866. *Holophagus gulo* Egerton : Huxley, p. 26, pl. 6.
1868. *Holophagus gulo* Egerton : Egerton, p. 502.
1872. *Holophagus gulo* Egerton : Huxley, p. 36, pl. 10.
1891. *Undina gulo* (Egerton) Woodward, p. 411, fig. 53.
1941. *Undina gulo* (Egerton) : Schaeffer, fig. 9*f*.

DIAGNOSIS. A *Holophagus* of large size, attaining a length of some 70 cm. Length of head about a quarter of the total length of the fish. Dorsal fins well developed.

HOLOTYPE. Fish, wanting head ; Geological Survey Museum, No. 28832 from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H.

DESCRIPTION. *The skull.* There is only one specimen in the B.M.N.H. (P 2022*a*) showing the roofing bones in dorsal aspect, but their general shape can be made out from laterally crushed skulls (Text-fig. 55). The parieto-dermopterotics extend back on to the opercular and the postero-lateral corners are produced. The parieto-dermopterotics are separated from the frontals by a distinct suture, and in life these two bones must have connected by ligaments, thereby giving a movable joint as in other Coelacanths.

The frontals appear to form part of a continuous sheet until they meet the antorbital and the premaxillae. On one or two specimens there are doubtful cracks on the frontals anteriorly which may have been sutures, and in which case would have denoted the presence of the nasals. However, the sheet appears continuous up to the premaxillae and antorbitals, and there is no clear demarcation to denote the presence of separate nasals.

From the lateral borders of the lower surfaces of this sheet a series of bones surround the orbits. These are the supraorbitals (parafrontals) of which there are five, and the most anterior articulates with the antorbital in front and the postorbito-infraorbital bar beneath. The antorbital itself is a large bone with a branch of the sensory canal running through it. From its position and extent it probably represents the fusion of two ossifications, the antorbital and the postrostral. Beneath the antorbital is a characteristically-shaped bone noted by Watson (1921 : 330). It abuts on to the premaxilla anteriorly and the postorbito-infraorbital posteriorly. It is hollowed out beneath, and produced downwards at its anterior extremity. Watson (1921 : 330) has observed a similar bone in *Macropoma mantelli* Agassiz, and has suggested that these forward processes " perhaps separated the two nasal apertures ". However, by analogy with other previously described Coelacanths, and from the course taken by the sensory canal through this bone, I believe it to be correctly termed the rostral. Anterior to the rostral the premaxilla can be seen on specimen B.M.N.H. P 2022. The premaxillae are not fused as in *Macropoma*, but are separate and bear several large teeth (3–4).

The postorbito-infraorbital (lacrymo-jugal) is a complete bar beneath the orbit similar in shape to that in *Holophagus acutidens.* Anteriorly it articulates with the supraorbital and the antorbital.

The arrangement of the postorbitals and other cheek plates is somewhat different from that figured by Reis (1892*a*, fig. 1) for *Holophagus acutidens*, and also different from that figured by Woodward (1891, fig. 53) for *Holophagus gulo* itself. Fitting neatly beneath the posterior corner of the postorbito-infraorbital and covering the quadrate is a triangular-shaped bone, tapered anteriorly. This is homologous to the preoperculoquadratojugal of Stensiö (1937 : 12), and the preopercular of Moy-Thomas (1937 : 387). Above this bone and articulating with both it and the postorbito-infraorbital is a somewhat larger bone, the preoperculo-postorbital. Between the preoperculo-postorbital and the parieto-dermopterotic is a postorbital bone, smaller than the other two cheek plates, and articulating with the first supraorbital.

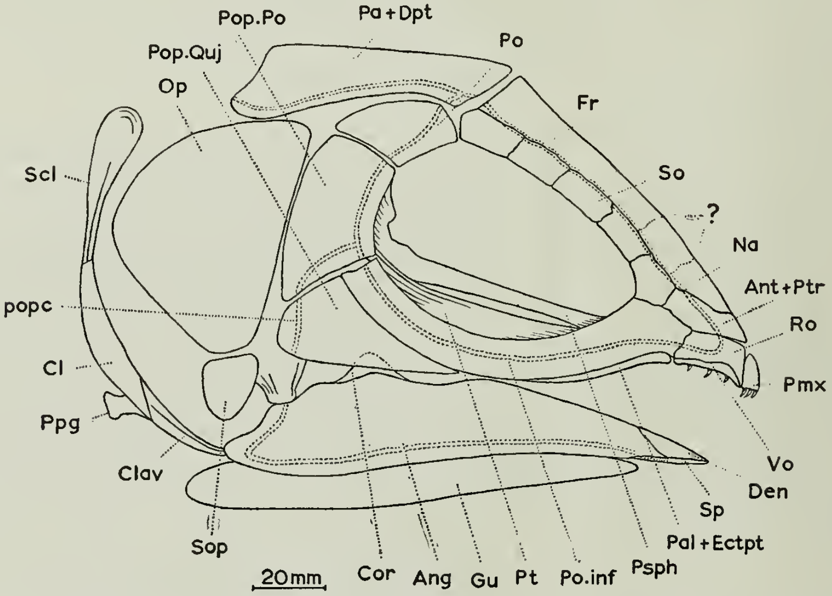

FIG. 55. *Holophagus gulo* Egerton. Reconstruction of the skull and pectoral girdle.

Behind the cheek plates is a large, roughly triangular-shaped opercular, well shown in B.M.N.H. P 3344. Beneath the opercular are traces of another small bone, presumably equivalent to the suboperculum of Reis (1892*a*, fig. 1). There is no evidence of a sclerotic ring, although this is present in the closely related *Holophagus acutidens.*

Lower jaw. In medial view the major portion of the lower jaw can be seen to consist of one bone, the angular (Text-fig. 56). This bone is continuous near its posterior end and no demarcation into a surangular can be found. Anteriorly it abuts on to the splenial and the dentary. These two bones are of approximately the same size, but are both much smaller than in other Coelacanths, particularly *Holophagus acutidens.* The position of the prearticular can be seen from Text-fig. 56. The coronoid appears to be much nearer the posterior end of the jaw than in other species of *Holophagus* being quite close to the articulatory facet. Between the rami of the jaws is a pair of delicately ornamented gular plates.

Neurocranium. The neurocranium can be seen in B.M.N.H. P 2022*a*, which shows the posterior portion of a dorso-ventrally flattened skull. In this specimen it is possible to recognize the basioccipital, prootic and basisphenoid in dorsal aspect (Text-fig. 57). The basioccipital forms a deep concave sheet, which projects behind the skull. It appears very similar to that figured by Aldinger (1930, fig. 6) for *Holophagus acutidens.* The prootic, which is continuous with the basioccipital, is a much smaller ossification and forms the main portion of the lateral walls of the neurocranium. Between the two prootics lies a large basisphenoid (this bone can also be recognized in B.M.N.H. P 2022). It is a stout ossification compared with the other bones, and its outer surface is convex, as though it were an articulating surface rather reminiscent of mammalian occipital condyles. The two foramina recognizable in the basisphenoid posteriorly transmitted the sixth nerve.

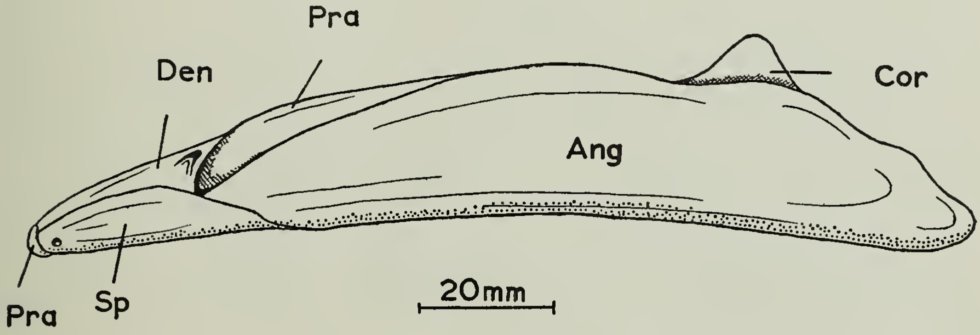

FIG. 56. *Holophagus gulo* Egerton. Restoration of lower jaw, based mainly on specimens B.M.N.H. P 2022 and P 3344.

The parasphenoid as it leaves the basisphenoid is comparatively narrow (B.M.N.H. P 2022), but as it runs forwards it becomes more spatulate. The neurocranial structure is generally very similar to that described for *H. acutidens* by Aldinger (1930 : 24) and also very similar to that described for *Macropoma mantelli* by Watson (1921, fig. 1).

Palate. On the articulated specimens little could be made out of the palatoquadrate apparatus. However, specimen B.M.N.H. P 9842 from the Great Oolite, Kingsthorpe, Northampton, consists of an isolated right pterygo-quadrate (Pl. 42). From its size it can probably be correctly assigned to the species *Holophagus gulo*, and as such will be described.

The major portion of the palate is formed by an enlarged pterygoid ; this bone (Pl. 42) is rather unusual in shape and quite different from that of any Coelacanth so far described. It is triradiate anteriorly, with a strong median ridge running well forward. Its dorsal edge is distinctly concave and also extends well forward, in contrast to the more upright nature of the pterygoid seen in other Coelacanths (*Axelia, Wimania, Macropoma, Nesides* etc.). Dorsally it articulated with the metapterygoid. On its inner surface the pterygoid bears small tubercular teeth, but these are restricted to the lower edge and upper rim. On the outer surface the quadrate is completely fused with the pterygoid, in the postero-ventral corner, but the quadrate can be clearly recognized from its distinctive ossification, with radiating lines running forwards (Pl. 42).

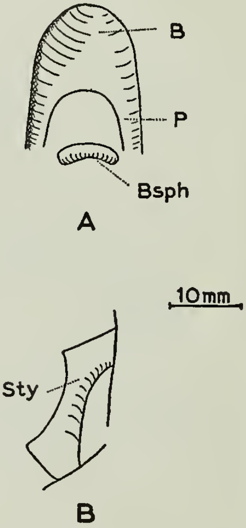

FIG. 57. *Holophagus gulo* Egerton. A, dorsal view of neurocranium. From B.M.N.H. P 2022*a* ; B, stylohyal, from B.M.N.H. P 3344.

A pterygo-quadrate from an obviously distinct species is shown in Pl. 43. It is B.M.N.H. P 959 from the Stonesfield Slate, near Oxford. It is much more elongated posteriorly, and its lowermost edge, which abuts on to the ectopterygoid and autopalatine, is very much shortened.

The palatine, ectopterygoid and vomers can only be seen on the majority of the specimens in lateral view. They project down beneath the postorbito-infraorbital bar, and run forwards to the maxillae. The ectopterygoid is the most posterior and is long and delicate, bearing very small teeth. This bone is often termed the maxilla, but Watson (1921, fig. 1) recognized it as a true ectopterygoid. In front of this bone are two similar ossifications, both bearing minute teeth. The first is the palatine and the most anterior the prevomer (pre-ethmoid of Stensiö, 1921, fig. 19).

Behind the opercular in B.M.N.H. P 3344 is a stoutish bone, almost hour-glass in shape and nearly vertical in position. This bone is the stylohyal (Text-fig. 57), but no other remains of the branchial arches could be found.

Sensory canal system. The main cephalic division of the sensory canal runs round the edge of the parieto-dermopterotic and no supratemporal commissure is recognizable in the posterior region, hence this compound sheet of bone does not contain the extrascapular. Just before it leaves the parieto-dermopterotic and passes into the frontal, the sensory canal branches to give the infraorbital canal. The infraorbital canal passes downwards through the postorbital and through the anterior edge of the preoperculo-postorbital. In the latter bone it gives off the preopercular sensory canal posteriorly. The infraorbital canal continues on through the length of the postorbito-infraorbital and into the rostral. Here it turns upwards and through the antorbital and into the lateral ventral edge of the nasal as the supraorbital canal. The supraorbital canal runs back up through the length of the frontal, its course being marked by pits both in the lateral edge of the frontal and in the dorsal edges of the supraorbitals. It finally fuses with the main cephalic division in the antero-lateral corner of the parieto-dermopterotic. The preopercular canal runs diagonally down through the preopercular-postorbital. The latter canal continues on down through the posterior edge of the preoperculo-quadrato-jugal bone.

The mandibular canal is marked by a double series of pits, and enters the lower jaw dorsally near the articulation. At first the canal runs backwards and downwards, but it then curves sharply round to run the length of the angular bone, and ends up in the splenial just short of the prearticular.

Appendicular skeleton. The pectoral girdle in both *Holophagus* and *Macropoma* has a backwardly directed portion of the endoskeleton attached to it. This bone shows no sutures in *Holophagus gulo* and probably represents the fusion of a scapula and coracoid. It occurs just posterior to where the cleithrum and clavicle articulate, and to it the skeleton of the pectoral fin must have been joined.

The girdle itself is complete and seen in B.M.N.H. P 2022 and P 3344. The supracleithrum is comparatively thin and rather spatulate in outline, with several strengthening ridges running down it. The cleithrum is of similar dimensions, and near its ventral extremity it has this short posteriorly-directed projection mentioned above. The clavicle runs on down from the cleithrum, and like the supracleithrum it has strengthening ridges along its length.

The pectoral fin has from fifteen to twenty fin-rays with a comparatively narrow insertion.

The pelvic plates of *Holophagus minuta* (Reis) (this is probably founded on young specimens of *Holophagus striolaris* (Münster)) and *Holophagus acutidens* have been well figured and it only remains to figure those of *Holophagus gulo* for comparison. The figure of Woodward (1891, fig. 53) is very misleading, and I have never seen a pelvic plate of *Holophagus gulo* looking anything like his drawing.

Anteriorly each plate is much expanded and sheet-like, with a strengthening ridge running down both of the lateral edges (Text-fig. 58). Although of much the same general shape, it differs in detail both from that found in *H. minuta* and in *H. acutidens*.

The pelvic fin shows seventeen to eighteen fin rays, but the insertion is larger than that of the pectoral fin.

Unpaired fins. The basal plate of the first dorsal fin is of typical Coelacanth form, triangular in shape with its apex directed forwards.

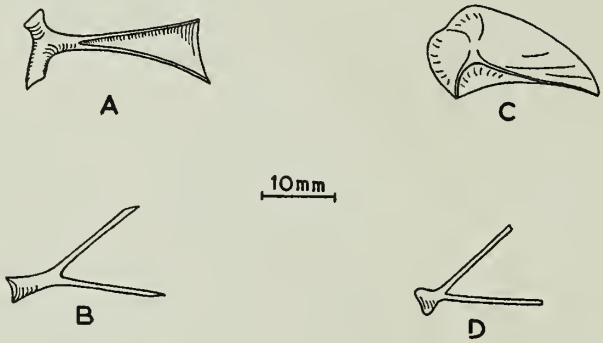

FIG. 58. *Holophagus gulo* Egerton. Plates supporting fins. A, pelvic plate; B, basal plate of anal fin, right side; C, basal plate of first dorsal fin, right side; D, basal plate of second dorsal fin, right side.

The fin itself is well developed with ten stout rays visible. The basal plate of the second dorsal fin is a bifurcated structure with the open part of the V directed forwards. Its fin has from fifteen to eighteen rays, with a broader insertion than that of the first dorsal.

Again the anal fin has a deeply bifurcated plate similar to that of the second dorsal fin. Schaeffer (1941 : 12) suggests that this type must have arisen by the development of an antero-ventral process from the posterior expanded division. There is no evidence of a median keel projecting ventrally as figured by Woodward (1891, fig. 53).

The fin is more delicate than the others and shows from between seventeen and eighteen fin rays, rather more slender and closely articulated distally.

Axial skeleton. The axial skeleton is as figured by Woodward (1891, fig. 53).

III. DISCUSSION

As an introduction to the discussion, a Table is given below listing the differences between the Palaeoniscoid condition and the condition found in the Holostei.

Palaeoniscoid condition	Holostean condition
1. Maxilla fixed, in articulation with the preopercular and postorbital bones.	1. Maxilla and preopercular reduced and completely separated. The preopercular is quite narrow dorsally while the maxilla only articulates with the snout.
2. Interopercular absent.	2. Interopercular present.
3. Suspensorium normally oblique.	3. Suspensorium vertical or slightly directed forward.
4. Coronoid process absent.	4. Coronoid process present.
5. Antorbital absent, nasals border orbit.	5. Antorbital present, nasals generally excluded from orbit.
6. Postrostral bone separates the nasals.	6. Postrostral bone only present in the early Semionotidae.
7. Pectoral and pelvic lepidotrichia usually completely segmented transversely.	7. Pectoral and pelvic lepidotrichia only distally transversely segmented.
8. Dorsal and anal fin-rays completely segmented transversely and are more numerous than the endoskeletal supports.	8. Dorsal and anal fin-rays partly segmented transversely and equalling the endoskeletal supports in number.
9. Clavicle present.	9. Clavicle absent.
10. Neurocranium completely ossified, individual bones fused and sutures not apparent.	10. Neurocranium either completely ossified or partially cartilaginous, in both cases individual bones clearly visible.
11. Tail unreduced and heterocercal.	11. Scaly lobe usually much reduced and tail hemiheterocercal or rarely homocercal.
12. Scales consists of three layers ; a lower layer of lamellated bone, and intermediate layer of dentine (cosmine), the whole capped by a layer of enamel. Canals of Williamson and dential tubules numerous.	12. Scales consisting of a lower layer of lamellated bone and an upper layer of enamel. Dentine layer and dential tubules normally missing. (*Lepidotes minor* still has dentine, Gross, 1935 : 48.) Canals of Williamson undergoing reduction.

The Origin and Affinities of the Holostei

The earliest Palaeoniscoid to show any development towards the Holostean condition is *Canobius*. It had already acquired an upright suspensorium by the Lower Carboniferous. Many later forms have also developed this vertical suspensorium quite independently of one another. Examples outside the Holostei proper include *Haplolepis*, *Pyritocephalus*, *Aeduella*, *Lepidopterus*, *Platysomus*, *Bobasatrania*, *Meridensia*, *Platysiagum* and all Parasemionotidae.

Other typically Holostean characters can also be found amongst the pre-Triassic fish fauna. *Phanerorhynchus* (Gill, 1923*a* : 465) shows a reduction in the number of fin-rays, whilst the general appearance of the trunk is distinctly Holostean. *Phanerosteon* (Fritsch, 1893) has the same number of radials as fin-rays and ossified vertebral centra resembling hollow cylinders, and *Pyritocephalus* and *Haplolepis* (Westoll, 1944) both show several Holostean characters besides an upright suspensorium. In most Palaeoniscoids and many Holosteans the supraorbital sensory canal remains separate from the infraorbital, but in the earliest Holostean *Acentrophorus* (see Text-fig. 69) the supraorbital canal fuses with the main cephalic division where it turns down as the infraorbital canal. This change-over from the first to the second type, clearly shown in the development of *Amia*, (Allis, 1889) has been independently achieved at least three times (Brough, 1936). Watson (1925 : 867) has shown it in the Palaeoniscoid *Oxygnathus ornatus* and Wade (1935 : 21, fig. 5) in the Catopterid *Brookvalia*.

The independent development of Holostean characters has already been emphasized within the group Subholostei by Brough (1936 : 388). Westoll (1937*b* ; 1944 : 98) working on *Aeduella* and the Haplolepids supports this view and states that it is reasonable to suppose that Holostean characters have been acquired independently in different forms. Again Stensiö (1932 : 295) stresses the resemblance between the Pholidopleuridae (Subholostei) and the later Pholidophoridae (Holostei). Further, Westoll (1944 : 67) points out the similarities between *Haplolepis ovoidea* and the generalized Holostean. He shows that the maxilla of *Haplolepis ovoidea* has lost all traces of its cheek expansion and that by very little modification it could be freed from the preopercular resulting in a thoroughly Holostean condition. The Haplolepids show beautifully that such developments can occur in closely allied fishes, and indicate the scale of changes necessary for the production of Holostean characters (Text-fig. 59).

The most significant difference between the Palaeoniscoids on one hand and the Holosteans on the other is this question of jaw suspensions. It is difficult to see why some of the Palaeoniscoids with their wide gape and much inclined suspensorium should change towards a more vertical jaw suspension. At first sight the Palaeoniscoid jaw appears to be perfectly adequate, and furnished with a continuous series of powerful teeth, there seems little reason for alteration. Regan (1923 : 460) and Watson (1925 : 868) both agree that the changes in the nature of the suspensorium took place in association with a change in habit of the fishes concerned, and Westoll (1937*b* : 576) suggests its correlation specifically with changes in feeding habits. However, once the upright suspensorium had been acquired, then innumerable subsequent alterations to a variety of other skull bones became possible. For example, the cheek bones were no longer needed to provide a rigid side wall to the skull in order to resist the stresses and strains of muscle action, but were free to develop independently. Westoll (1944, fig. 44) has already shown what remarkably different patterns of cheek bones can be produced in the Haplolepidae once an upright suspensorium had been acquired. Other changes intimately linked with the acquisition of an upright suspensorium included a change in position of the maxilla. This moved forwards and became free from the preopercular, and simultaneously other changes occurred in the region of the snout. The projecting rostrum is reduced and finally lost (Parasemionotidae), whilst other changes occurred in the palate. In the palate the upper margin of the pterygoid became separated from the maxilla, and once the quadrate had secured sufficient support, by connection between the metapterygoid, preopercular and hyomandibular, then the freeing of the maxilla became possible. In the Palaeoniscoid condition, the *musculus adductor mandibulae* was more or less horizontal, lying within the palatoquadrate-maxillary apparatus and lower jaw, and having its origin on the palatoquadrate. Later, with this change in support of the quadrate, the *musculus adductor mandibulae* shifted its origin to a much more backward and vertical position (on to the anterior rim of the preopercular). Finally,

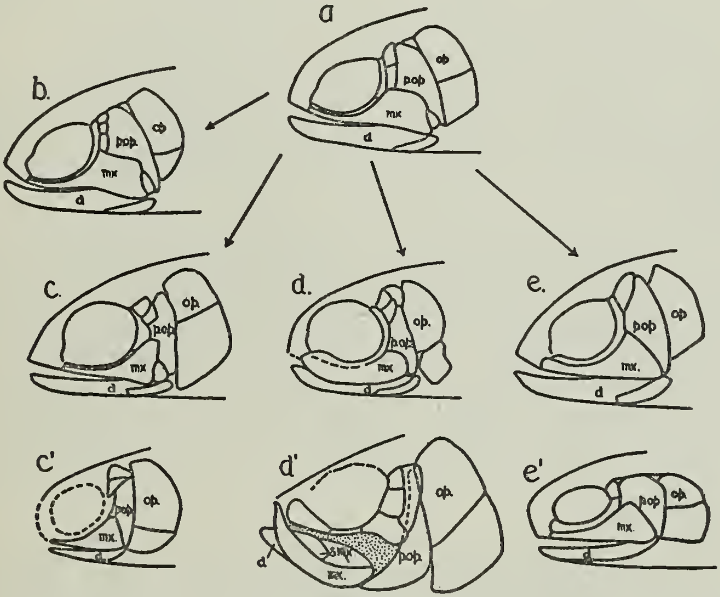

Fig. 59. Derivation of different Haplolepid cheek patterns, with examples of convergent structure in later Actinopterygians from Westoll (1944). a, cheek of X ; b, *Pyritocephalus sculptus* Fritsch ; c, *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry) ; *d*, *H.* (*H.*) *ovoidea* (Newberry) ; *e*, *H.* (*H.*) *corrugata* (Newberry) ; c^1, *Peltopleurus lissocephalus* Brough (after Brough) ; d^1, *Leptolepis coryphaenoides* Bronn (modified after Rayner) ; e^1, *Perleidus madagascariensis* Piveteau (after Piveteau).

the shortening of the mouth is accompanied by the formation of an interopercular, probably from the first branchiostegal ray (Piveteau, 1934 : 160). Stensiö (1932 : 98) put forward the suggestion that there was a definite functional correlation between the freeing of the maxilla and the modification of the dermal bones in the snout area, while Westoll (1944, fig. 47) has shown diagrammatically how it is possible to derive a Holostean type of cheek, snout and palate from a Palaeoniscoid one simply by alterations in the angle of the suspensorium and the reduction of the ventral parts of the snout.

The reasons and advantages of these changes are several and all closely interrelated. Undoubtedly the most important advance from the Palaeoniscoid condition was this freeing of the maxilla coupled with the straightening of the suspensorium. Once this had occurred then the swinging forward of the lower jaw became possible and with it a much more efficient means of food capture. On opening, the lower jaw could now protrude forwards in front of the upper, and by hinging of the remainder of the cheek apparatus, the sucking action so characteristic of the Teleosts was evolved, and prey instead of being actively hunted down could now be " gulped " into the mouth from a short distance. The freed double-hinged maxilla forming the outer and more backward boundary to the mouth thereby prevented the prey escaping, whilst the formation of a toothed premaxilla (from a fragmentation of the tooth-bearing rostral elements) was also an asset in this respect.

One of the main reasons for bringing about these changes can be related to similar occurrences in the tetrapods. Within the bony sheath formed by the palato-quadrate-maxillary apparatus there was little or no room for the adductor mandibulae muscle to " belly " out, thus the rigid walls of the cheek broke up to allow for this increased expansion.

Once this break up of the rigid cheek walls had occurred, then with only a moderate change in the insertion of the adductor mandibulae muscle, a much more powerful jaw action would be acquired (coupled with the development of a coronoid process on the lower jaw at about the same time). Thus the early Holosteans could now not only bite harder but were free to develop powerful crushing dentitions. Within the Holostei a powerful crushing dentition is met with in the Pycnodonts and Lepidotids, whilst the Palaeoniscid ancestors to the Pycnodonts, the Amphicentrids, have a similar but less robust dentition. These forms occupied the evolutionary niche vacated by the Dipnoi, and were responsible for the rapid decline of the Dipnoans in the early Mesozoic.

The question of the origin of the Holostei can be examined. Romer (1945 : 580) in his classification retains the super-order Holostei and within it the five orders : Amioidea, Semionotoidea, Pholidophoroidea, Aspidorhynchoidea and Pycnodontoidea. For the sake of convenience I shall adhere in this discussion to the broad lines of his classification, giving superfamily designation where he has used orders.

AMIOIDEA

The Holostei have been regarded by many authorities (Regan, 1904, 1923, 1929 ; Gregory, 1923, 1933) to be a uniform group of closely-related fishes, monophyletic in origin. Stensiö (1932 : 296) first put forward the idea that perhaps the Holostei were really a polyphyletic group, and this view has been supported by Brough (1939), Westoll (1944), Piveteau (1941) and Lehman (1952). Rayner (1941, 1948) considers the origin of the Holostei an open question, but appears to favour the monophyletic view. Schaeffer & Dunkle (1950 : 25) also believe the evidence to be inconclusive, but point out that the Semionotids, Amioids, and Pholidophoroids have essentially the same roof pattern, and on this and other evidence they suggest that Semionotids and Amioids had a common ancestral stock in the Permian, whilst the Pholidophoroids may have evolved from that same stock, possibly the Parasemionotids, at a later time.

Until the description of the Lower Triassic family the Parasemionotidae (Text-figs. 67, 68) by Stensiö (1932) and Piveteau (1934), all the Holostei were believed to have arisen from the same unknown Palaeoniscoid stock.

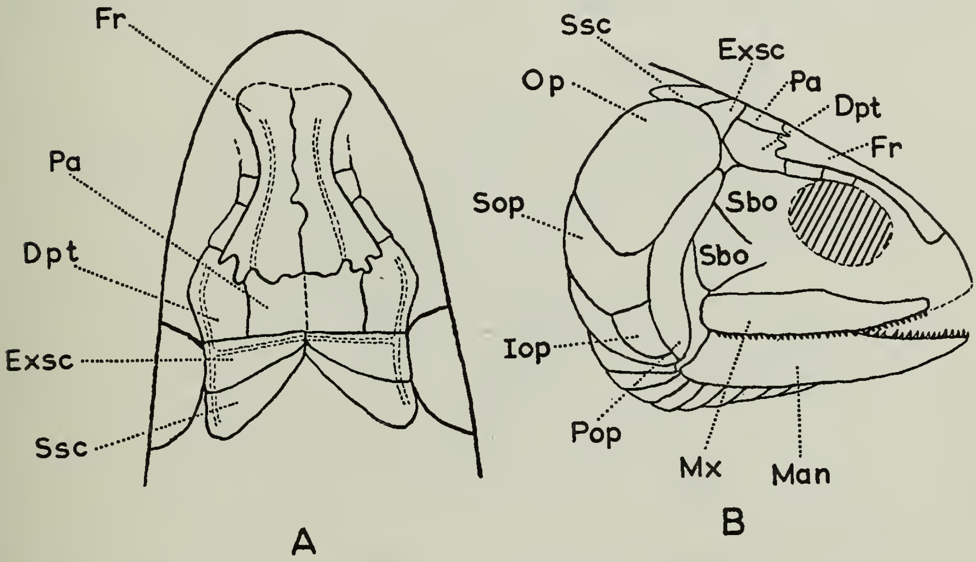

Fig. 60. *Eoeugnathus megalepis* Brough. Reconstruction of skull in A, dorsal view; B, lateral view. After Brough (1939).

The Parasemionotidae resemble the later Furidae (Text-fig. 60) in many details of skull structure. Brough (1939 : 91) first emphasized the unmistakable similarities between these two families, pointing out in both the identical small parietals and large dermopterotics, the similar relationships in size and shape of the extrascapular and suprascapular, the proportions of the frontals bordered in each by a row of supraorbitals, the similar dermosphenotics and the presence of large paired nasals. Both families have interoperculars and an almost identical jaw structure. In contrast to the Furidae the Parasemionotidae lack suborbitals and have a relatively unreduced preopercular.

Lehman (1952) has shown that in some Parasemionotids from the basal Trias of Madagascar suborbitals are being formed by anamestic fragmentation of the anterior part of the preopercular (see p. 340 for further details). Therefore he concludes that the Parasemionotids are probably ancestral to the Furids.

Since the Parasemionotidae arose from the Palaeoniscoids some time during the Permian (or even earlier), the Semionotidae must have arisen from the Palaeoniscoids independently of the Furidae for the following reasons :

(*a*) A typical Semionotid (*Acentrophorus*) exists in the Upper Permian.

(*b*) Early Furids resemble Semionotids less than later ones, and many of the resemblances between the Furidae and Semionotidae are due to convergence.

At this stage in the discussion it would be as well to look into the origin of the Holostean suborbitals (postorbitals). The first suggestion comes from Watson (1925 : 868) who states that the bone occurring in the Palaeoniscid *Coccocephalus wildi* between the anterior border of the preopercular and the infraorbital series may give some indication as to the possible source of the suborbital plates of the Lepidostei. Later (1928 : 58) he states that the series of three bones in *Elonichthys caudalis* and two in *Elonichthys serratus* (Text-fig. 75), which lie along the anterior edge of the preopercular (between it and the posterior infraorbitals) are the source for the suborbitals of the Holostei. Aldinger (1937 : 364) puts forward a different view. He considers that the Holostean suborbitals have arisen by a breaking up of the anterior expanded area of the Palaeoniscid-Subholostean preopercular. Further, he believes it to have occurred independently in several of the Palaeoniscids and Subholosteans. This is supported by the presence of supramaxillary and postmaxillary sensory lines on the preopercular of the Parasemionotidae while in some Holostei (*Lepidotes*, Westoll, 1957*a*, fig. 7), *Semionotus capensis* (Text-fig. 71) and

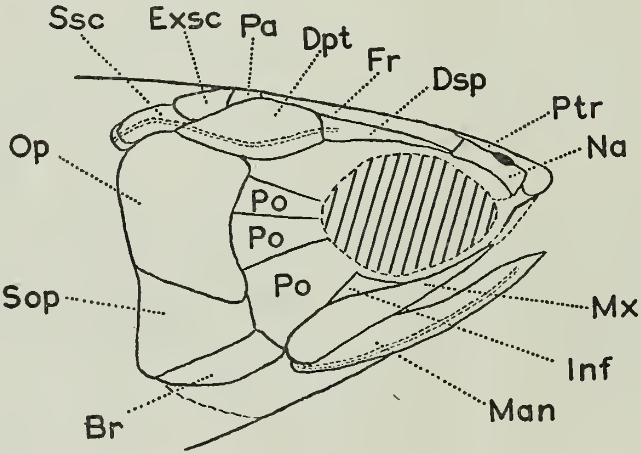

FIG. 61. *Ptycholepis curta* Egerton. Restoration of skull in lateral view. After Brough (1939).

Osteorachis macrocephalus (Text-fig. 24) they have become transferred to the suborbitals. Other evidence he cites includes the presence of a small bone beneath the preopercular in *Ospia* (Stensiö, 1932, fig. 84) and also three small bones above the preopercular in *Parasemionotus*. Aldinger links this breaking up of the preopercular with the acquisition of an upright suspensorium, but as Schaeffer & Dunkle (1950 : 19) point out, this theory does not explain the presence of suborbitals in forms like *Glaucolepis* (Nielsen, 1942, fig. 30) and *Palaeoniscus freieslebeni* (Aldinger 1937 : 102) which still retain an expanded preopercular, or in forms like *Canobius* (Moy-Thomas & Dyne, 1938 : 440) with an expanded preopercular and a vertical suspensorium.

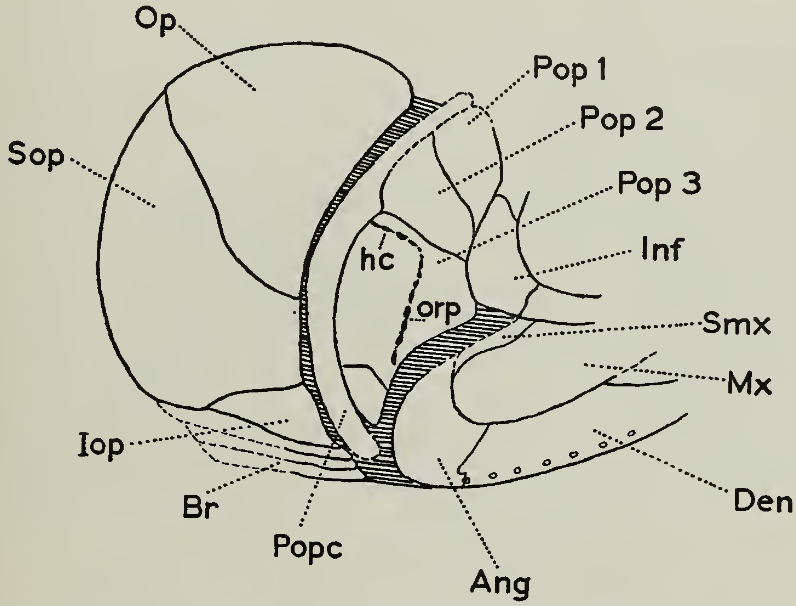

Fig. 62. *Thomasinotus divisus* Lehman. Fragmentation of the preopercular. From Lehman (1952).

Finally, Stensiö (1947 : 148) considers the suborbitals of the Palaeonisciformes and Subholostei to have been derived either from the anamestic components of the adjoining postorbital infraorbitals or from the anamestic anterior part of the preopercular, or from both sources. Thus he considers them not to be equivalent in the individual forms possessing them.

As to the origin of the Holostean suborbitals, Stensiö (1947 : 154) puts forward two theories. The first is that they arose by a subdivision of the anterior parts of the whole Palaeonisciform preopercular into independent minor plates. This is exactly comparable to the theory put forward by Aldinger (1937 : 363), and Stensiö bases it also on an interpretation of the three bones above the preopercular in *Parasemionotus* as being suborbitals derived from the anamestic components of the preopercular. His second theory is that the suborbitals of the Palaeoniscids and Subholostei have been directly inherited (Watson, 1925 : 868 ; 1928 : 58). For these suborbitals to acquire the Holostean condition, Stensiö (from an interpretation of Brough's, 1939 : 66, description of *Ptycholepis curta* ; Text-fig. 61) suggests that they underwent an excessive outgrowth backwards, over the anterior portion of the preopercular, which was consequently reduced. Then as the anterior portion of the preopercular was eliminated, the superficial sensory lines (supramaxillary and postmaxillary) carried thereon would have been forced to shift to the skin laterally to the suborbitals, and would thus become secondarily situated outside these bones. Schaeffer & Dunkle (1950 : 21) summing up the evidence, believe that the palaeontological data alone would favour Stensiö's second theory for the origin of Holostean suborbitals.

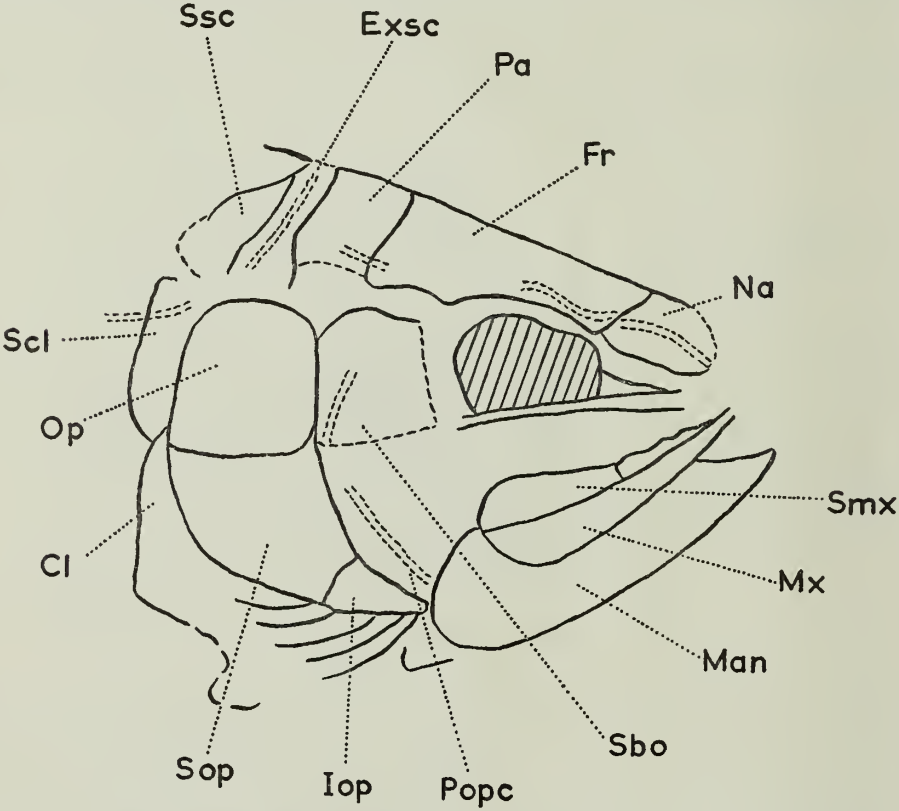

FIG. 63. *Promecosomina formosa* (Woodward). Skull in lateral view, after Wade (1941).

In 1952 Lehman described three new Parasemionotid genera from the basal

Trias of Madagascar. These were *Stensiönotus*, *Jacobulus* (Text-figs. 62, 67) and *Thomasinotus*. In his description Lehman shows that the preopercular in all three forms shows division into different plates and that the disintegration of the anterior portion of the preopercular as proposed by Aldinger (1937 : 363) and Stensiö (1947 : 154, 1st hypothesis) really took place. In fact there are true suborbitals present as Brough (1939 : 93) suspected. Having shown that fragmentation and reduction of the preopercular were taking place in the Parasemionotidae, Lehman proves beyond doubt that the Parasemionotid stock must have been ancestral to the Furidae and hence the entire Amioidea. Further he proves that in the Furid stock of Holosteans, the suborbital series arose by anamestic fragmentation of the preopercular.

Together with the three new forms, the basal Trias of Madagascar has yielded five genera belonging to the family Parasemionotidae : *Watsonulus*, *Parasemionotus*, *Stensionotus*, *Jacobulus* and *Thomasinotus*, and Lehman lays emphasis on the very rapid evolution which this family must have been undergoing in the early Trias. Other genera included in the family Parasemionotidae are the two forms from the basal Trias of Greenland, *Broughia* and *Ospia* described by Stensiö (1932). The reception of these last two genera in the Parasemionotidae has been justified by Stensiö's (1937) subsequent discovery of a true interopercular in some of the Ospiids. Lehman (1952 : 185) also called attention to the similarity between the Parasemionotidae and the Promecosominidae. From a study of Wade (1935, 1941) he suggested that since *Promecosomina* has a divided preopercular, both halves of which contain a portion of the preopercular canal (see Text-fig. 63), the dorsal division of this bone could not be a suborbital plate as Wade (1941, fig. 1) labelled it. Lehman therefore concluded that *Promecosomina* was a true Parasemionotid and that the family Promecosominidae must be abandoned, with which view Wade (1953 : 72) later agreed. In order to test the validity of his conclusion, I examined some samples of *Promecosomina*.

Genus ***PROMECOSOMINA*** Wade, 1935

DIAGNOSIS. See Wade, 1935 : 80 ; 1941 : 380.

TYPE SPECIES. *Promecosomina formosa* (Woodward).

Promecosomina formosa (Woodward)

(Text-figs. 63, 64)

1908. *Acentrophorus* sp. Woodward, p. 21.
1908. *Semionotus formosus* Woodward, p. 23, pl. 4, fig. 8.
1908. *Pholidophorus australis* Woodward, p. 26.
1935. *Promecosomina beaconensis* Wade, p. 80, pl. 8, figs, 3, 4 ; text-fig. 46.
1941. *Promecosomina formosa* (Woodward) Wade, p. 382, pl. 17 ; text-figs. 1–3.
1953. *Promecosomina* Wade, p. 72.

DIAGNOSIS. See Wade, 1935 : 80 ; 1941 : 382.

HOLOTYPE. Specimen in the Australian Museum, Sydney, F 38905, figured by Woodward, 1908, pl. 4, fig. 8, an imperfect fish lacking pectoral fins from the Hawkesbury Series at St. Peters, N. S. Wales, and counterpart in the B.M.N.H. P 18091.

MATERIAL. Specimens in the B.M.N.H.

DESCRIPTION. *The skull.* These specimens came from the Upper Trias (Hawkesbury) of St. Peters, N.S.W. A reasonably complete dorso-ventrally flattened skull roof can be seen on B.M.N.H. P 18072, in which the parietals, frontals, nasals, dermopterotics, extrascapulars and suprascapulars are all visible. The parietals are small, paired and nearly square in outline (Text-fig. 64). On either side are the elongated, narrow dermopterotics. The frontals, which are broad posteriorly, narrow between the orbits. Anteriorly the nasals abut on to the premaxillae as can be seen in B.M.N.H. P 18092, but the state of preservation is too poor to be able to discern teeth on the latter bone. Adjoining the hinder margin of the parietals is a pair of triangular extrascapulars. These meet on the mid-line in a short suture. Behind the extrascapulars are the well-developed suprascapulars. These bones are also triangular and extend posteriorly well back over the anterior region of the trunk. In front of the opercular is a long preopercular curved gently forwards at its lower end. Throughout its length it is narrow and the preopercular canal runs through it, as can be seen on several of the B.M.N.H. specimens, as a calcite cast. Anterior to the preopercular is a pair of suborbital plates. These are both quadrangular in general shape, and the more dorsal member often completely overlaps the dorsal region of the preopercular. Specimens which show clearly both suborbital and preopercular plates are, B.M.N.H. P 18091, P 18092 and P 18093. Although Wade (1941 : 386) could find little evidence of a circumorbital series, a complete one did exist, as is shown by B.M.N.H. P 18091. With difficulty a small dermosphenotic,

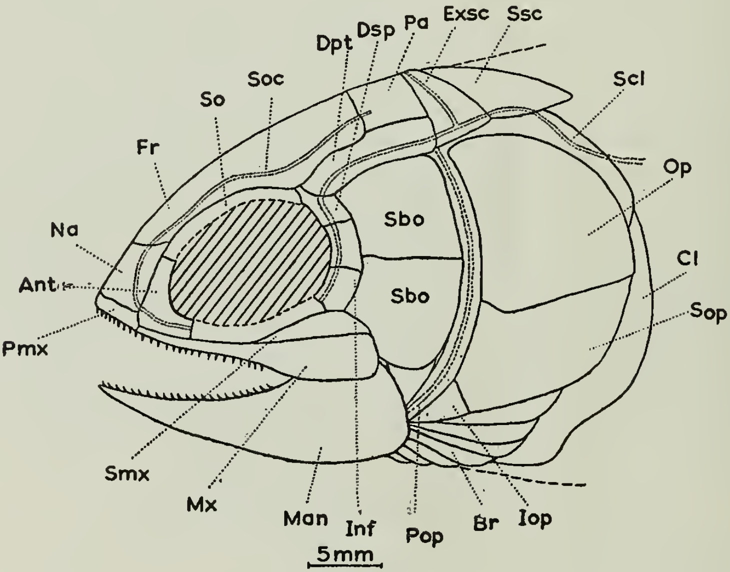

FIG. 64. *Promecosomina formosa* (Woodward). Reconstruction of skull in lateral view.

lying beneath the dermopterotic and anterior to the dorsal suborbital, can be made out on this specimen. Below it are two further members of the infraorbital series, limiting the orbit posteriorly. The exact number of these infraorbitals cannot be ascertained. The anterior region of the snout is well shown in B.M.N.H. P 18092. The antorbital is large and abuts on most of the posterior edge of the nasal, and ventrally meets the premaxilla and maxilla. There is evidence of a supraorbital series, but the number of individual bones cannot be ascertained. The sensory canal system of the head is as Wade (1941 : 387, fig. 1) described, except that the infraorbital sensory canal travels down through the dermosphenotic and round the infraorbital series into the antorbital, whence it appears to pass up into the nasal as the supraorbital canal. An adequate description of the remainder of the skull and body is given by Wade (1935, 1941).

It is clear that *Promecosomina*, with its well-developed suborbitals overlapping the preopercular, is more advanced than the earlier Parasemionotids. *Promecosomina* is a good freshwater Holostean and the family Promecosominidae must be retained for its inclusion. It resembles the Furidae in its fusiform trunk with an almost straight dorsal edge, in the slight forward inclination of the suspensorium and the accompanying moderate curvature of the preopercular, the long maxilla, well-developed supramaxilla and the interopercular which does not reach far forwards. Thus, like the Furidae, it was undoubtedly descended from the Parasemionotidae and can be correctly placed with the former in the Amioidea.

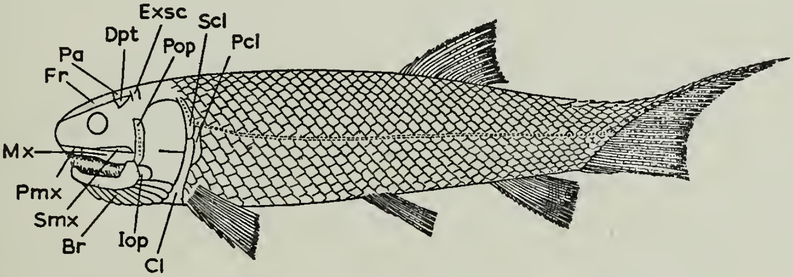

FIG. 65. *Tungusichthys acentrophoroides* Berg. From Berg (1941).

Fairly closely allied to the Parasemionotidae is the family Tungusichthyidae erected by Berg (1941 : 461) to include the solitary genus *Tungusichthys* (Text-fig. 65) from the Lower Trias of the Tunguska Coal Basin, Siberia. This family differs from the Parasemionotidae in possessing a narrow vertical preopercular (very similar to that found in the Furids) and in the shape of the frontals and maxillae. The caudal fin is almost homocercal and from the few known facts about the family there is much to be said for associating it with the Parasemionotidae in the super-family Ospiiformoidea.

Thus the Parasemionotidae is a large group, whose origin is somewhat obscure. Brough (1939 : 94) suggested their derivation from a Palaeoniscoid such as *Pteronisculus*. This is impossible since *Pteronisculus* already has a suborbital series present (formed probably from a division of the infraorbitals). Again this rules out several other of the Palaeoniscoids with a more or less upright suspensorium and a suborbital series. Piveteau (1941 : 88) postulates a relationship between the Parasemionotidae and the Perleidids. It is possible that these two groups had a common ancestral stock in the Permian.

Returning to the Amioidea : the family Furidae forms the central group of the Mesozoic Holosteans, and bears close relationship to the later Amiidae (Brough, 1939 ; Rayner, 1941, 1948 ; Schaeffer & Dunkle, 1950). The group as a whole shows a rather conservative history, culminating in the more specialized Macrosemiids and Pachycormids. The evolutionary trends within the Macrosemiids have been discussed at length by Saint-Seine (1949 : 287). The Pachycormidae which Rayner (1941 : 229) finds too specialized to include with any other family and with which view Westoll (1944 : 85) agrees, have been shown by Lehman (1949 : 39) to have unmistakable Amioid resemblances, despite several pronounced specializations.

Observations on the neurocrania of *Caturus*, *Heterolepidotus* and *Osteorachis* by myself, bear out Lehman's (1949 : 39) conclusions. Rayner (1948 : 296) in her study of *Caturus*, from the available material was unable to decide whether or not there was an independent ossification in the posterior otic region (i.e. a Holostean opisthotic). However, I have been able to recognize in *Caturus chirotes* a separate ossification in that area. The ossification is interpreted by me as an opisthotic (Text-fig. 36). In *Osteorachis* the brain case is solidly constructed, and consequently sutures are difficult to recognize, but each ossification is distinct, with the bone fibres radiating in a regular fashion from the centre of the ossification. Thus it is again possible to distinguish a separate ossification, above the intercalar in the posterior otic region, and this bone must be an opisthotic (Text-fig. 26). The same bone also occurs in a similar position in *Heterolepidotus* (Text-fig. 29). In comparison, the neurocrania of *Pachycormus* (Rayner, 1948, figs. 18, 30) and *Hypsocormus* (Stensiö, 1935, fig. 6) both have an opisthotic present in the lateral wall. One other point of similarity between the neurocrania of the Pachycormidae and the Furidae is the absence of a supraoccipital. In conclusion, a comparison with the neurocrania of *Sinamia* (Stensiö, 1935, figs. 1, 2) and *Amia* must be made. In both these forms the opisthotic is missing. This is not considered to be of primary importance, but rather to be connected with a progressive lightening of the skull as a whole in *Sinamia* and *Amia*. Lastly, as Lehman (1949 : 40) indicates, in the general skull structure, shape of parasphenoid, the course of the arteries and the pharyngeal supports, *Pachycormus* seems closer to *Amia* than to any other of the Amioidea.

One remaining genus, placed by Piveteau (1941 : 78) in the Semionotidae is *Paracentrophorus*. It comes from the Lower Trias of Madagascar and according to his description it is more primitive than the earlier *Acentrophorus*. However, it has not accomplished the reduction of its tail from the heterocercal to the hemiheterocercal state in the same manner as the rest of the Semionotids. With this in view I have redescribed the genus to try to ascertain its true relationship.

Genus *PARACENTROPHORUS* Piveteau, 1941

Diagnosis. See Piveteau, 1941 : 77–88.

Type species. *Paracentrophorus madagascariensis* Piveteau.

Paracentrophorus madagascariensis Piveteau

(Text-fig. 66)

1941. *Paracentrophorus madagascariensis* Piveteau, p. 78, pl. 10, figs. 1–6 ; text-figs. 7–10.

Diagnosis. As for genus.

Syntypes. The three specimens figured by Piveteau (1941, pl. 10) from the Lower Trias of Madagascar.

Material. Specimens in the B.M.N.H., from the Lower Trias of Bobasatrana, NE. Madagascar.

Description. *The skull.* In the skull the suprascapular is of normal proportions, but the extrascapular is broad and the parietals are large and squarish as in the Semionotidae. There is no median suprascapular (unlike *Acentrophorus*), and the dermopterotics are not as large as in *Acentrophorus* but they have the same rounded expansions of their outer borders anteriorly. The frontals are stout and of the same proportions as those in *Acentrophorus*, but are not completely fused, a distinct suture being visible. The frontals meet the paired nasals anteriorly. The nasals are stout ossifications, meeting in the mid-line, with the rostral, a small element between their anterior extremities and the premaxillae. The nasals bound a large nasal orifice anteriorly, while the antorbital completes the posterior edges. Of the shape of the premaxilla there is only very fragmentary evidence. The antorbital is a large bone somewhat hour-glass shaped, with a widened ventral area. The opercular is higher than broad, larger than the subopercular and the suture between them has the characteristic course, turning sharply upwards anteriorly. There is a distinct interopercular and the preopercular is narrow and gently curved. The preopercular has definitely not acquired the true Seminotid condition, where it is elongated in the lower region and extends far forward. In front of the preopercular are three recognizable suborbitals, the most ventral being the largest. The suborbital series is very similar to that found in the Amioidea. The maxilla is stout and long with a small supramaxilla at its posterior apex. There is a regular series of teeth along the length of the maxilla ; these are of medium size and pointed. The maxilla extends from just above the ventral extremity of the preopercular to the end of the orbit, where it meets the premaxilla. Along the anterior rim of the suborbitals are three infraorbitals and together with two more along the dorsal edge of the maxilla they bound the orbit behind and beneath. The dermosphenotic is large, much larger than in the Semionotidae generally, and probably represents the fusion of the dermosphenotic and supraorbital. There is only one supraorbital anterior to the dermosphenotic and there is apparently a gap between it and the succeeding antorbital. The mandible bears similar teeth to those of the maxilla, and beneath and behind the lower jaw is a complete set of branchiostegal rays, the most posterior rays being somewhat enlarged.

Sensory canals. The sensory canal system is as Piveteau (1941 : 81) described, except that I have been able to trace the infraorbital canal from the anterior corner of the dermopterotic, through the posterior extremity of the dermosphenotic and then round the infraorbitals into the antorbital. Here it gives off a branch dorsally which runs up through the length of the antorbital. The canal continues forwards probably into the rostral (this region is not clearly represented in any specimen) and back up through the nasal as the supraorbital canal.

Pectoral girdle and fin. The pectoral girdle is a stout ossification. From the suprascapular the supracleithrum runs back to midway down the opercular. Through the supracleithrum runs a continuation of the sensory canal system out on to the body scales as the lateral line. The cleithrum is large and stout and distinctly concave anteriorly. The primary pectoral girdle was not observed, but there are four stout radials on which the lepidotrichia of the pectoral fin articulated. Between the cleithrum and the supracleithrum is a single postcleithrum. All the above information was obtained by taking moulds in a plastic material called " Vinamould " from the original specimens in the B.M.N.H. (P 16245–6, P 19560–1, 62–3, 64–5, 70–1, 72–3).

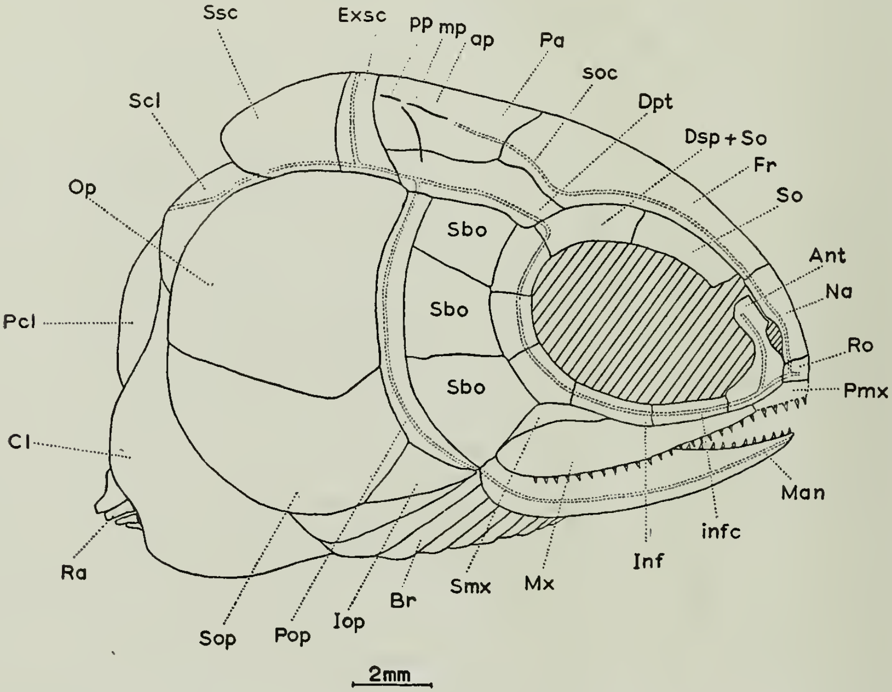

FIG. 66. *Paracentrophorus madagascariensis* Piveteau. Reconstruction of skull in lateral view.

From this description it is clear that *Paracentrophorus* is not at all closely related to either *Acentrophorus* or the later Semionotidae. The main differences in skull pattern include the nature of the preopercular, the unreduced maxilla and the stout nasals meeting in the mid-line in *Paracentrophorus*. Another major difference is the method of reduction of the heterocercy in the tail which is achieved in *Paracentrophorus* in the same way as in the Furid line. Minor differences include the absence of fin fulcra in *Paracentrophorus*, the position of the anal fin which is much nearer the tail in *Paracentrophorus*, and the somewhat high insertion of the pelvic fins. Further, unlike the Semionotidae the back is not depressed behind the insertion of the dorsal fin.

Thus there is a good case for putting *Paracentrophorus* in its own family the Paracentrophoridae and in placing this family not in the Semionotidae, as Piveteau (1941 : 77) has done, but in the Amioidea.

PHOLIDOPHOROIDEA

The next major group of Holostean fishes, the Pholidophoroidea, were those with the greatest evolutionary potential and from them arose the Teleosts, the dominant fishes of the present day. The earliest known Pholidophorid is alleged to come from the Middle Trias (Stolley, 1920 : 75), but Saint-Seine (1949 : 291) has cast doubt on this interpretation of a fish from the Muschelkalk of Germany. However, despite this, fragmentary remains for the most part referable to the genus *Pholidophorus* do come from Middle Trias deposits (*P. oblongus* Bellotti ; *P. obsoletus* Costa).

Stensiö (1932 : 164) has shown how the Pholidopleurids approach the Pholidophorids in structure, but indicates that the former group cannot be by any means considered ancestral to the latter. Further researches by Lehman (1952 : 145) into the structure of *Australosomus* has proved this to be correct, and it seems certain that the Pholidopleuridae represent a side branch, well off the main line of Holostean ancestry. Saint-Seine (1949 : 292) draws analogies between the Pholidophoridae and the Parasemionotidae, but concludes that the characters exhibited by the Parasemionotidae are too far removed from the condition found in the Pholidophoridae for direct descent to be possible. It has been shown below that there are many close resemblances between the families Parasemionotidae and Pholidophoridae, so much so that I have no hesitation in postulating the derivation of the Pholidophoridae direct from the earlier Parasemionotidae. The skull structure of the Pholidophoridae has long been considered similar to that of the Amiidae, but as Rayner (1937, 1948) has shown, the neurocrania differ considerably. If ancestry from the Parasemionotidae be accepted, these changes in the pattern of the neurocranial bones will have had time to have become apparent. A comparison of the Parasemionotidae with the Pholidophoridae is given below (p. 350) in tabular form (See also Text-figs. 67, 68):

From this comparison we see that the major differences between the two forms lie in first the preopercular and secondly the orbital series. The preopercular in *Thomasinotus divisus* Lehman (1952, fig. 129) (Text-fig. 62) is narrow and curved and contains the preopercular canal. It would need to become more curved anteroventrally and broadened in that region to approach the condition found in the

Pholidophorids. However, in front of this preopercular in *Thomasinotus divisus* there are three large plates acquired by the anamestic fragmentation of the anterior edge of the preopercular. In *Jacobulus novus* the anterior portion of the preopercular is similarly fragmented, only into two large plates. In both these genera the most posterior plate is the larger and contains both the supra- and postmaxillary sensory lines. In *Pholidophorus* sp. Westoll (1937, fig. 8, *d*) has shown that the most ventral plate of the circumorbital series (representing probably suborbital and infraorbital) has both these sensory lines present in it, and it appears probable that the large suborbitals in the Pholidophoridae have arisen by the anamestic fragmentation of the Parasemionotid preopercular. In *Leptolepis* and *Pholidophorus* there are five

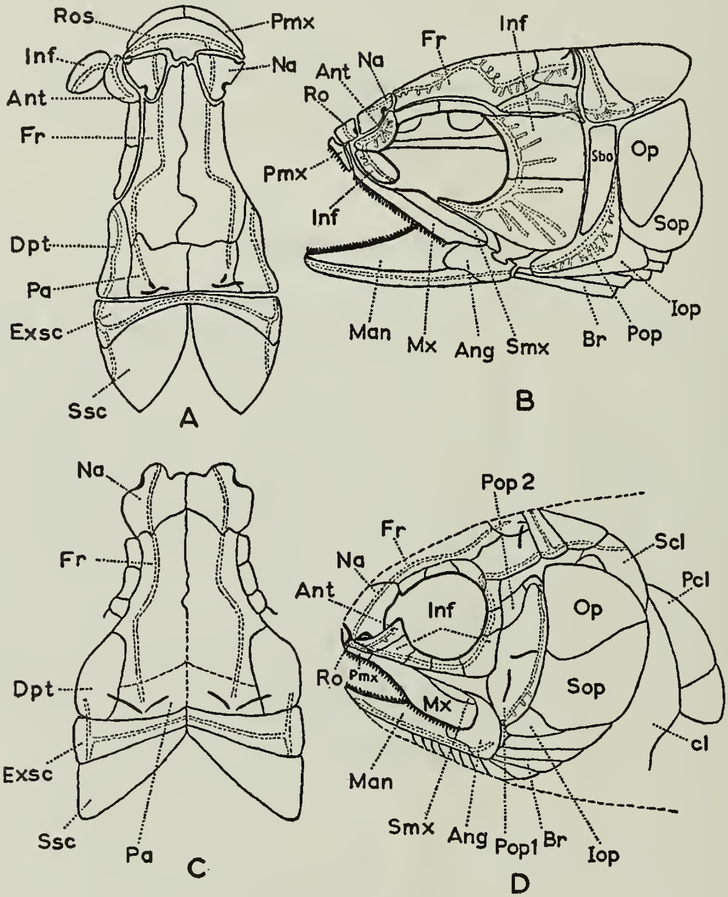

FIG. 67. A, *Pholidophorus similis* Woodward, dorsal view of skull, after Saint-Seine (1949); B, *Pholidophorus similis* Woodward, lateral view of skull, after Saint-Seine (1949); C, *Jacobulus novus* Lehman, dorsal view of skull, after Lehman (1952); D, *Parasemionotus labordei* Lehman, lateral view of skull, after Lehman (1952).

infraorbitals, and of these the most posterior ventral is large and extends backwards over the anterior medial part of the preopercular (Text-fig. 68). Therefore it probably represents an infraorbital plate fused with one of the ventral suborbital plates. Beneath the eye in the Pholidophoridae the infraorbitals have become reduced to a narrow strip round the sensory canal, but this is a structural adaptation and is of no great importance. Schaeffer & Dunkle (1950 : 21) have shown the variation in the circumorbitals and suborbitals that can take place at the specific level within the genus *Pholidophorus* and this only adds further weight to the previous arguments. Further if the opisthotic in the neurocranium of the Amioidea is homologous with the autopterotic of the Pholidophoroidea, which is what I suspect, then a common

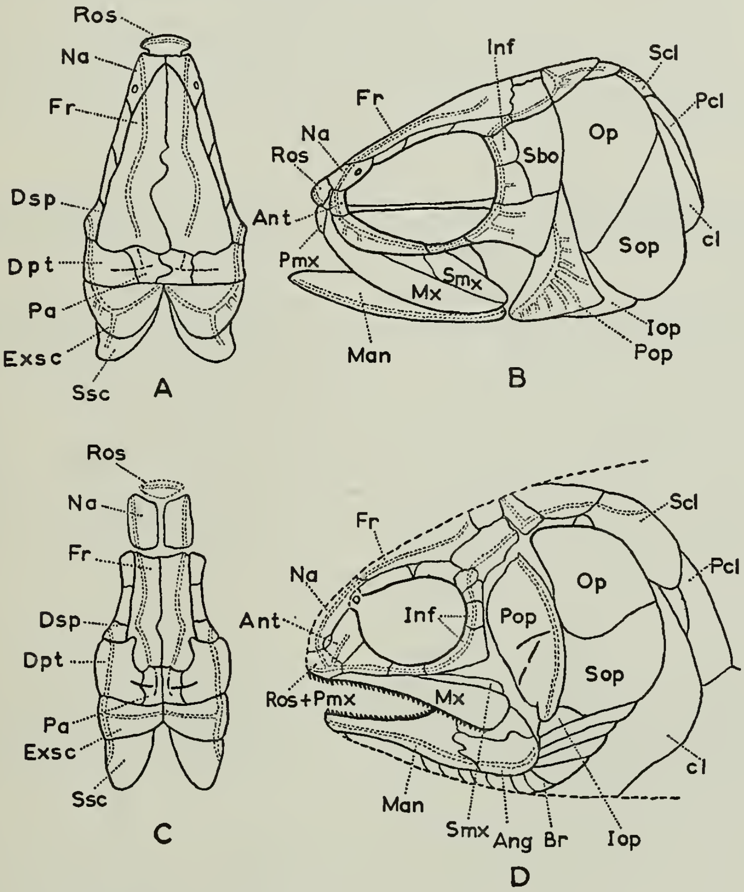

Fig. 68. A, *Pholidophorus bechei* Agassiz, dorsal view of skull, after Rayner (1948) ; B, *Pholidophorus bechei* Agassiz, lateral view of skull, after Rayner (1948) ; C, *Watsonulus eugnathoides* (Piveteau), dorsal view of skull, partly after Piveteau (1934) ; D, *Watsonulus eugnathoides* (Piveteau), lateral view of skull, after Lehman (1952).

ancestry for both groups (from the Parasemionotidae) is even more certain. From all these facts it appears obvious that the Pholidophoridae have arisen directly from the Parasemionotidae.

In the superfamily Pholidophoridea I include the families Pholidophoridae, Leptolepidae, Protelopidae, Archaeomaenidae, Oligopleuridae and Pleuropholidae.

The progression Pholidophorid-Leptolepid-Teleost has been satisfactorily demonstrated by Rayner (1941, 1948) and Saint-Seine (1949); (see p. 316). Saint-Seine (1949 : 290–295) points out that while the Protelopids (*Eoprotelops*) specifically foreshadow the Teleost family Elopidae, the Leptolepids may be directly ancestral to the Chirocentridae.

Parasemionotid		Pholidophorid
1. Parietals small and squarish, median pit line long, extending well into the dermopterotic.	.	1. Parietals small and square, with a long median pit line, extending into the dermopterotic.
2. Dermopterotic larger than the parietal.	.	2. Dermopterotic of comparable size and shape to that of Parasemionotid.
3. Dermosphenotic small.	.	3. Dermosphenotic small.
4. Extrascapular narrow.	.	4. Extrascapular generally narrow.
5. Suprascapular enlarged, especially in *Watsonulus eugnathoides* (Text-fig. 68).	.	5. Suprascapular enlarged, especially in *Pholidophorus similis* (Text-fig. 67).
6. Rostral present with a rostral commissure.	.	6. Rostral and rostral commissure present.
7. Antorbital in *Watsonulus eugnathoides* and *Parasemionotus labordei* (Text-fig. 67) approx. bounds both nasal orifices ventrally, and has an upward branch of the sensory canal running through it (triradiate). This branch gives off several finer ones posteriorly.	. .	7. Antorbital almost identical in size and shape and position. In *Pholidophorus similis* there is a comparable branch of the sensory canal (triradiate) with several finer posterior branches. Further, the antorbital more or less bounds the two nasal orifices ventrally.
8. Nasals large, rectangular, meeting in mid-line.	.	8. Nasals smaller, triangular and the nearest approach to their meeting in the mid-line can be seen in *Pholidophorus bechei* (Rayner, 1941) where they do still meet anteriorly (Text-fig. 68).
9. Maxilla completely free, and its posterior end has moved downwards. Supramaxilla present.	.	9. Maxilla comparable in shape and position, supramaxilla present.
10. Opercular slung well back, anterior ventral corner has moved upwards and backwards. The suture between it and the subopercular follows a characteristic course.	.	10. Opercular again similar, a little larger but slung upwards and backwards. The suture line between it and the subopercular follows a similar course to that in *Parasemionotus*.

11. Subopercular larger than opercular.	11. Subopercular slightly smaller than or of comparable size to the opercular.
12. Preopercular large, although undergoing anamestic fragmentation in some genera.	12. Preopercular very different in shape and position.
13. Interopercular present.	13. Interopercular present.
14. Circumorbital series complete, do not vary much in size.	14. Circumorbital series complete, some plates of which are very much expanded —others reduced.
15. Suborbital series just forming.	15. Suborbital series well developed.
16. Mandible composed of three bones.	16. Mandible has only two bones, surangular reduced.
17. Sensory canals well developed, the supraorbital canal running right back into the parietals.	17. Sensory canal system very similar, with the supraorbital canal passing right on to the parietal.
18. Cleithrum expanded ventrally, postcleithra present.	18. Cleithrum similar, single postcleithrum normally present.
19. Clavicles present.	19. Clavicles absent.
20. Gular plate present.	20. Gular plate present.

However, it would seem from the scale structure of *Pholidophorus* and *Leptolepis* that the progression Pholidophorid-Leptolepid-Teleost is not a strictly correct one. Although many of the Clupeoids, in particular the Chirocentridae, can be derived from a Leptolepid stock, such families as the Elopidae would on scale structure alone appear to have been derived more satisfactorily from a Pholidophorid ancestor. This idea of deriving some at least of the Teleosts direct from the Pholidophorids is not a completely new one. Woodward (1942 : 908) has already pointed out that the peculiar expanded ridge-scutes behind the pelvic fins of the Clupeoid *Diplomystus longicostatus* indicate a derivation from a Pholidophorid rather than a Leptolepid, since in the latter ridge-scutes are unknown. However the presence or absence of ridge-scutes is such a variable character that little importance can be attached to it. Again, the Salmonidae can be derived much more easily from a Pholidophorid ancestor than from a Leptolepid one, not just on scale structure, but on general skull disposition, in particular the make-up of the jaws which from the outset are far too specialized in the Leptolepids. Likewise the Characinidae probably also originated from an early Pholidophorid stock.

Thus the most primitive Teleost families can be straightforwardly derived from either the Pholidophorids or from the Leptolepids. One thing appears certain, they could not have been derived from any other known Holostean family, despite the opinion of Woodward (1942) to the contrary. I must agree with Rayner (1948 : 338) that from my own observations I can find no support in the morphology of the skull to derive the Teleost from any other source.

The Archaeomaenidae includes the genera *Archaeomaene*, *Aphnelepis*, *Aetheolepis* and *Madariscus* all described by Wade (1941*a*) from the Jurassic of Australia. This family bears a very close resemblance to the Pholidophoridae not only in the general shape of the body but in the construction of the skull, especially the lower and upper jaws. A few differences are apparent between, for example, *Archaeomaene* and *Pholidophorus*. In the former the vertebrae are ossified, resembling more the ring-like structure seen in some of the later Leptolepids, and there is a considerable variation in the circumorbital series. Despite these there is a close relationship between the Archaeomaenidae and Pholidophoridae, and they must have come from the same stock.

The two remaining families which I have included in the Pholidophoroidea for the sake of convenience, the Oligopleuridae and the Pleuropholidae present taxonomic difficulties. The Oligopleurids have been placed slightly off the Pholidophorid-Leptolepid line of evolution by Rayner (1941 : 232), but she indicates that they show numerous advances parallel to those of the Leptolepids. The high coronoid process, the fused vertebral elements, and thin scales are all similar to the former group, but the Oligopleurids still have fin fulcra and other peculiarities. The Pleuropholids are even further removed, but it seems probable that both these families took their origins from the same stock of the Parasemionotids that gave rise to the Pholidophorids.

SEMIONOTOIDEA

The third group of Holosteans is the Semionotoidea. The earliest member of this superfamily is the Permian genus *Acentrophorus*. The Semionotoidea do not constitute a major part of the Mesozoic fauna and did not give rise to other groups, owing to their early somewhat precocious specialization. Previously the Semionotids were believed to have given rise to all the later Holostean groups (Tate Regan, 1923 ; Gregory, 1923). Brough (1939 : 108) although excluding the Semionotids from the ancestry of the Furids, thinks that these two groups may have had a common ancestor in the Permian. Schaeffer & Dunkle (1950 : 18) support this view, pointing out that " It would appear less radical to derive a Semionotid from a Parasemionotid type than from any other known Palaeoniscid or Subholostean ". Schaeffer & Dunkle came to this conclusion after suggesting that both Gill (1923*b*, fig. 3) and Gregory (1933, fig. 21*b*) were wrong in their interpretation of the snout region of *Acentrophorus*, and that so far as it is known the Semionotid snout has a dermal bone pattern like that of the Parasemionotids. Because of this apparent discrepancy in interpretation it was decided to re-examine both *Acentrophorus* and *Semionotus*.

Genus *ACENTROPHORUS* Traquair, 1877

Diagnosis. See Woodward, 1895*b* : 51 and Gill, 1923*b* : 20.

Type species. *Acentrophorus varians* (Kirkby).

Acentrophorus varians (Kirkby)

(Text-figs. 69, 70, 72)

1862. *Palaeoniscus varians* Kirkby, p. 267.
1864. *Palaeoniscus varians* Kirkby, p. 353, pl. 18, fig. 2.
1877. *Acentrophorus varians* (Kirkby) Traquair, p. 565.
1895*b*. *Acentrophorus varians* (Kirkby) : Woodward, p. 51.
1923*b*. *Acentrophorus varians* (Kirkby) : Gill, p. 19, figs. 1–3, 5, 7–11.
1933. *Acentrophorus varians* (Kirkby) : Gregory, p. 124, fig. 21*b*.
1939. *Acentrophorus varians* (Kirkby) : Moy-Thomas, p. 120, text-fig. 32*b*.

Diagnosis. See Woodward, 1895*b* : 52 and Gill, 1923*b* : 20.

Holotype. Imperfect fish, Hancock Museum, Newcastle, from the Magnesian Limestone (Upper Permian), Durham.

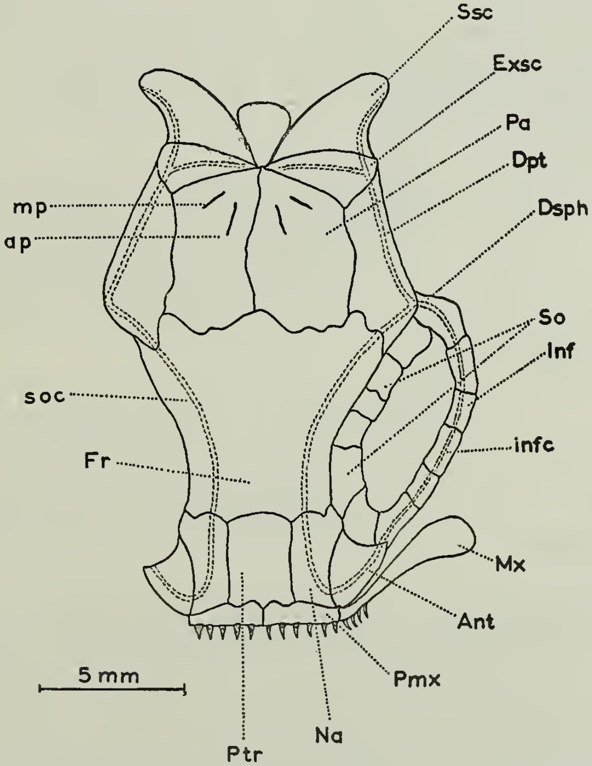

Fig. 69. *Acentrophorus varians* (Kirkby). Reconstruction of the skull roof in dorsal view, mainly from specimens P 593, P 594, P 597 in Professor Watson's collection.

DESCRIPTION. Through the kindness of Professor Watson I was enabled to examine a superb set of specimens of this genus contained in his collection. From these and from specimens in the B.M.N.H. a clear picture of the structure of the skull roof of *Acentrophorus* (Text-fig. 69) was built up. My own observations agree very closely with those of Gill (1923*b* : 25). The bones of the cranial roof are shown in Text-figs. 69, 70. The parietals are large, rectangular in shape and bear short median and anterior pit lines. The two parietals together form roughly a square over the neurocranium. On either side of the parietals are the somewhat elongated dermopterotics, roughly the same size as the parietals and having a rounded expansion of their outer borders anteriorly. The frontals are completely fused, and no suture line could be observed. They form a stout ossification, broad posteriorly, but narrowing between the orbits. Anteriorly the frontals abut a median, rectangular postrostral

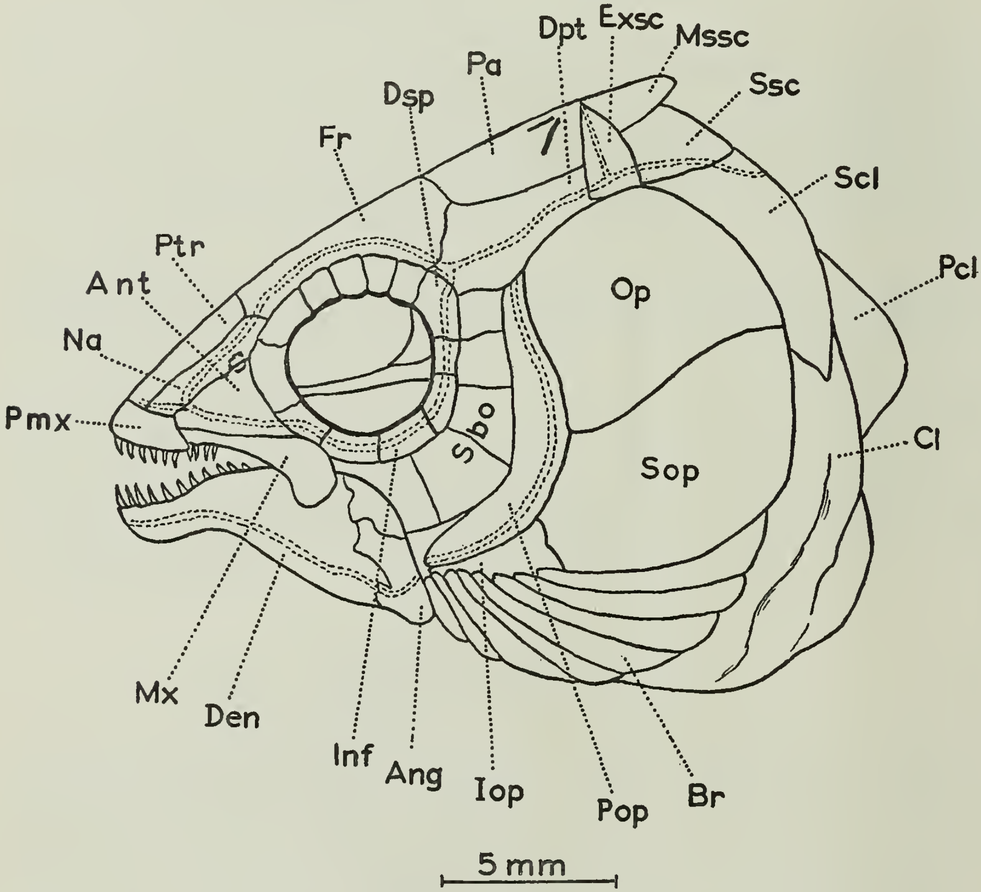

FIG. 70. *Acentrophorus varians* (Kirkby). Lateral view of skull, partly after Gill (1923*b*).

element (or possibly postrostral + rostral fused). The postrostral is a single, thin ossification showing no trace of a median division, and represents the paired nasals of Gill (1923*b* : 24) and the paired postrostrals of Gregory (1933, fig. 21*b*). On either side of the postrostral occur the nasals. These are a little smaller than the postrostral, and posteriorly articulate with the frontals, while anteriorly they meet the paired premaxillae. Fitting into the lateral edge of the nasal is a smaller triangular bone, the antorbital (rostral of Moy-Thomas, 1939, fig. 32*b*). The large orbit is surrounded by a chain of circumorbitals and a dermosphenotic, all of much the same size. Adjoining the hinder margin of the parietals is a pair of elongate, triangular extrascapulars, which do not quite meet in the mid-line. Behind the extrascapulars is a pair of well-developed suprascapulars, with a median element between them. The sensory canal system of the head is much as Gill described it (1923*b* : 28). The main cephalic division of the canal enters the posterior end of the suprascapular from the supracleithrum, and runs forward giving off the supratemporal commissure, which traverses the extrascapular, and then continues forward as far as the orbit, where it turns sharply downwards via the dermosphenotic, to form the infraorbital canal. The supraorbital canal joins the main cephalic division where it turns down as the infraorbital canal (i.e. in the dermopterotic) and then runs back through the frontal and nasal, curves sharply through the antorbital and links up again with the infraorbital canal. In the anterior postrostral region there were some traces of a rostral commissure, but this area was too crushed for definite interpretation.

Genus ***SEMIONOTUS*** Agassiz, 1832

DIAGNOSIS. See Woodward, 1895*b* : 55.

TYPE SPECIES. *Semionotus bergeri* Agassiz.

Semionotus capensis Woodward

(Text-fig. 71)

1888*c*. *Semionotus capensis* Woodward, p. 138, pl. 6, figs. 1–5.
1895*b*. *Semionotus capensis* Woodward : Woodward, p. 58.
1901. *Semionotus capensis* Woodward : Schellwein, p. 1, pl. 1 ; pl. 2, figs. 1–4.
1909. *Semionotus capensis* Woodward : Broom, p. 262.
1915. *Semionotus capensis* Woodward : Hennig, p. 49, pl. 3.
1957. *Semionotus capensis* Woodward : Guffroy, p. 847, pl. 28 ; text-figs. 2, 3.

DIAGNOSIS. A Semionotid of moderate size, fusiform in shape with a slender pedicle to the tail. Length of the head and opercular apparatus make up a quarter of the total body length. Dorsal fin arising in the middle of the back, which is depressed behind the point of insertion. Dorsal fin with approximately twelve lepidotrichia, the anal fin with less, approximately eight. Body scales smooth, not serrated.

SYNTYPES. Four nearly complete fishes on one block partly in counterpart, B.M.N.H. P 4089, from the Stormberg Beds, Ficksberg, Orange Free State.

MATERIAL. B.M.N.H. and Professor Watson's collection.

REMARKS. A further study was made of this species from the Cave Sandstone

(Upper Triassic) to supplement that description of *Acentrophorus*, and to see whether or not the structure of the nasal region of *Acentrophorus* was unique amongst the Semionotidae.

DESCRIPTION. *The skull.* The parietals in this genus are large and square, with an anterior and posterior pit line near the posterior boundary (Text-fig. 71). The dermopterotic is smaller than in *Acentrophorus*, the frontals longer and not completely fused with one another. Anteriorly the frontals are pointed and have a V-shaped space between them into which the postrostral bone fits. The postrostral is much narrower than in *Acentrophorus* and is a very thin ossification. On each side of the postrostrals are the nasals and again these are smaller than in *Acentrophorus*. Between the nasals and the circumorbital series is one other smaller bone, an antorbital. The supraorbital series of bones totals five, whilst the infraorbitals together with the dermosphenotics number seven. There are four suborbitals of which the most posterior member is the largest. The second suborbital carries a groove in which lay the anterior division of the supramaxillary line : in the fourth suborbital a more vertical groove contained the postmaxillary line during life. The preopercular is very much curved ventrally and throughout its length runs the preopercular canal. The remainder of the skull and body is very close to Schellwein's (1901) description. The sensory canal system of the head, however, shows several differences from that described in *Acentrophorus*. The main cephalic division commences in the supracleithrum, runs through the supra- and extrascapulars, gives off the supratemporal commissure in the latter bone, runs across the dermopterotic and turns down through the dermosphenotic and carries on round the infraorbital series as the infraorbital canal. The supraorbital canal does not join the main

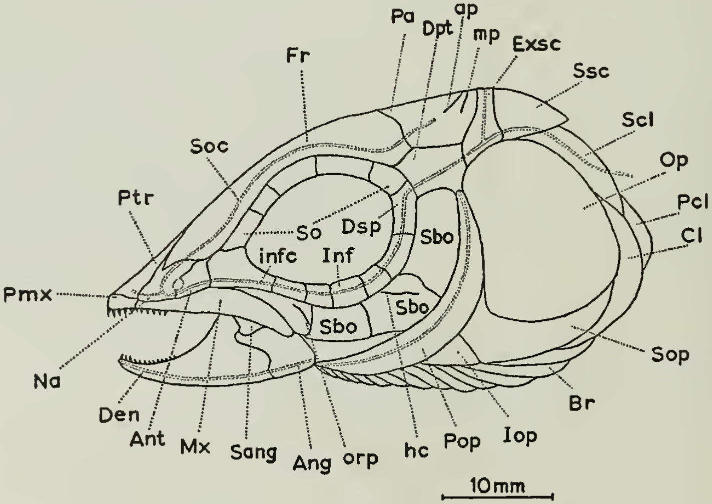

FIG. 71. *Semionotus capensis* Woodward. Reconstruction of skull in lateral view, mainly after B.M.N.H. P 10985, P 9486, P 6861 and P 4089.

cephalic division posteriorly, but commences in the parietal and runs down through the frontal, then into the nasal, where it turns sharply back into the antorbital to join with the infraorbital canal. There is just the semblance of a connection between the infraorbital and the supraorbital canals posteriorly, a line of irregular pores passing from the dermosphenotic to the supraorbital canal in the posterior frontal region. Where the sensory canal traverses the nasal it gives off a branch anteriorly, which passes forward into the postrostral. This represents the rostral commissure. The bone I have called the postrostral, from its position and extent, represents, then, a fusion of two elements, the rostral and postrostral. In *Acentrophorus* this ossification is large and separates the nasals widely. In the early Semionotids such as *Semionotus capensis* from the Cave Sandstone, this bone is reduced and posteriorly forms only a narrow strip separating the nasals (and overlies the posterior extensions of the premaxilla). Finally, in the later Semionotids such as *Lepidotes* and *Dapedium* it no longer separates the nasals but is reduced to a small ossification anterior to them. This small ossification is termed a rostral by Rayner (1948, fig. 10) and Schaeffer & Dunkle (1950 : 7), and is probably a correct interpretation, since the postrostral portion will have been the region to have undergone the reduction.

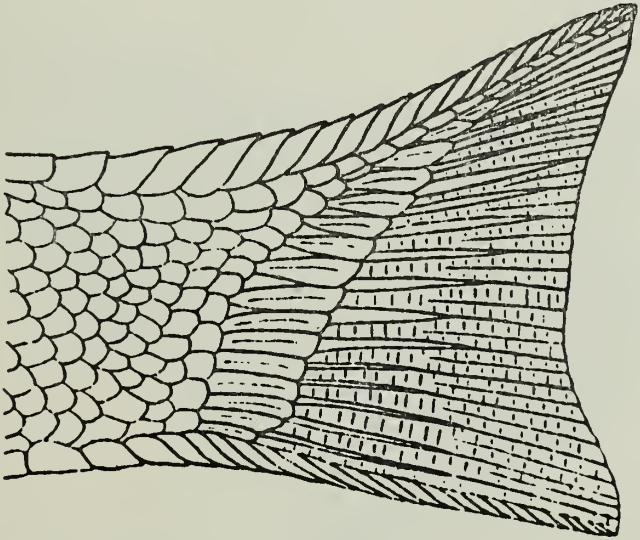

FIG. 72. *Acentrophorus varians* (Kirkby). Caudal fin. From Gill (1923*b*).

From these two descriptions it is obvious that the earliest Semionotid, *Acentrophorus*, differs markedly from the Parasemionotidae. In the Parasemionotidae the nasals are paired and meet in the mid-line, with a small rostral element between their anterior extremities and the premaxillae. The condition in *Acentrophorus* has already been described, wherein a large median postrostral completely separates the nasals. Turning to the circumorbital series, in the Parasemionotidae there are few bones, while in *Acentrophorus* there are as many as twelve. The remaining structures of the cheek are also quite different in the two forms. *Acentrophorus* already has a complete series of suborbital bones in the Permian, yet anamestic fragmentation of the preopercular has only just started in the Parasemionotidae by the Lower Triassic. Other major differences include the shape of the preopercular, which in *Acentrophorus* has already acquired the very specialized Semionotid condition, being distinctly curved and directed right forwards ventrally. The gape is consequently much shorter in *Acentrophorus*, and the lower jaw has moved forwards. Both the suprascapular and the dermopterotic are widened and enlarged. These points alone are sufficient to demonstrate that the two groups were derived independently from the Palaeoniscoidea, and further that their Palaeoniscoid ancestors were not at all closely related.

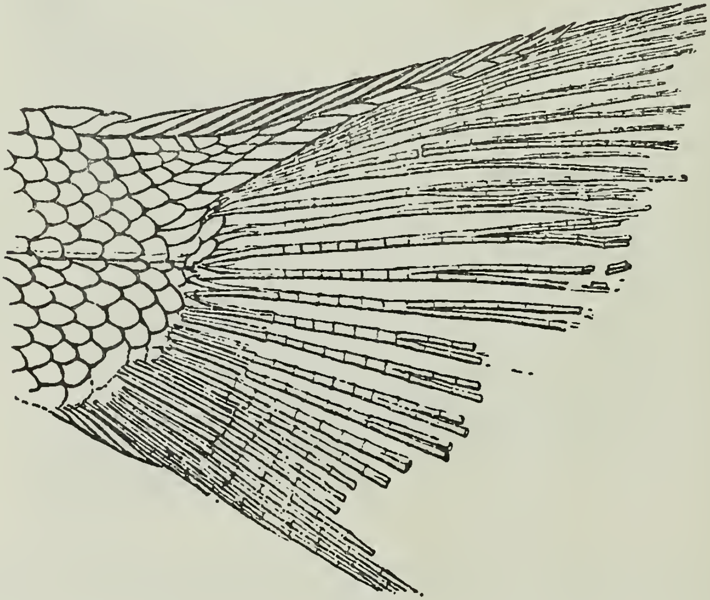

Fig. 73. *Dapedium orbis* Agassiz. Tail of a young individual. From Gill (1923*b*).

Other evidence for deriving the Semionotoidea direct from the Palaeoniscoids is to be found in the caudal region. The tail of *Acentrophorus* (Text-fig. 72) is completely heterocercal with the most dorsal row of scales complete, and extending to the tip of the tail. Gill (1923*b*, figs. 15, 16) has shown that in the Semionotidae this reduction of the tail from an ancestral heterocercal state to a hemiheterocercal form has taken place by the removal of longitudinal rows of scales from below upwards. *Acentrophorus* still retains the most dorsal row of scales complete, which extend to the tip of the tail, while in a young specimen of *Dapedium* (Text-fig. 73) Gill (1923*b*, fig. 16) has shown that the most dorsal row of scales was still prominent, extending about two-thirds of the distance to the tip. In the Parasemionotidae a different method was employed, the caudal lobe being reduced by the removal of transverse rows from the tip of the tail.

One final feature is the difference in the ossification of the neurocranium in the adult Amioid and Semionotid. In the Parasemionotidae the neurocranium of the mature individual is a single ossification in the postorbital region (Stensiö, 1932 : 227 ; Lehman, 1952 : 160), but in the Semionotidae (Rayner, 1948, fig. 30 and Text-fig. 74) this region is made up of discrete paired and unpaired ossifications. In *Lepidotes* (Text-fig. 44) the individual bones are distinct, and there was much cartilage present. In *Dapedium* the neurocranium is far more heavily ossified, although the individual bones can still be recognized (Text-fig. 39).

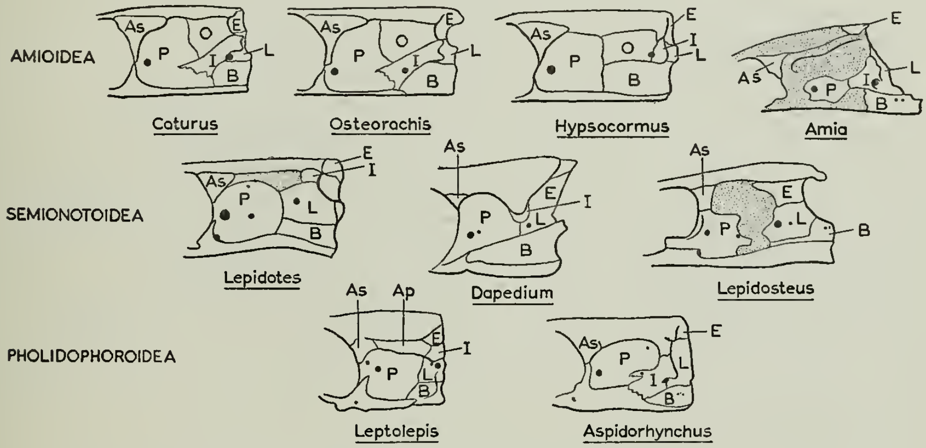

FIG. 74. Holostean neurocrania in lateral view, diagrammatic. *Leptolepis* and *Aspidorhynchus* from Rayner (1948).

In most of the adult Palaeoniscoids so far described in the literature, the postorbital region of the neurocranium is represented by a single ossification. However, in the immature specimen of *Cosmoptychius striatus* described by Watson (1928 : 49) the neurocranium shows several separate ossifications, whilst Westoll (1944 : 95) claims to have evidence of more than one ossification in a specimen of *Cheirolepis*. Other Palaeoniscoids described with separate neurocranial ossifications include *Birgeria* (Stensiö, 1921, 1937), *Elonichthys* (Rayner, 1948 : 331), and *Pteronisculus* (*Glaucolepis*, Nielsen, 1942 : 92). It is most probable then that the single ossification of the postorbital region of many of the adult Palaeoniscids and Subholosteans developed from several centres of ossification which have become completely fused.

Comparing now the structure of the neurocranium of the Semionotoidea with that seen in the Amioidea, none of the Semionotids so far described has an opisthotic present in its neurocranium whereas I have already established its presence (p. 286) in the Amioidea. Thus this absence of an opisthotic in the Semionotoidea separates them neatly from the Amioidea which possess this bone in at least the earlier members. There can be little doubt that the Amioidea and Semionotoidea arose from different Palaeoniscoid stocks.

Apart from the presence or absence of the opisthotic, the similar construction of the neurocrania in the Semionotoidea and Amioidea, and for that matter in the remainder of the Holostei, is due to the retention in the different ancestral stocks of a basic pattern present in the embryonic ossifications of a large number of Palaeoniscoids and Subholosteans. This view was put forward by Westoll (1944 : 95) and appears to be the only one by which the more or less homogeneous nature of the neurocrania within the Holostei (established by Rayner, 1948) can be explained.

The Semionotoidea range from the Upper Permian to Recent, and within the group several distinct evolutionary trends can be recognized. From the basic form, typified by *Acentrophorus* and *Semionotus*, one line has developed by deepening of the body and skull to give such forms as *Dapedium* and *Tetragonolepis*, while another has undergone elongation to give the very fusiform *Lepidosteus*.

The neurocranium of *Dapedium* has been described (Text-figs. 38, 39, 40), and it differs from that of *Lepidotes* in being much more solidly ossified and in possessing a supraoccipital. Woodward (1893 : 564) first recognized the presence of a supraoccipital in *Dapedium*, but Rayner (1948 : 307) disagrees with him, suggesting that the process called supraoccipital by Woodward is in fact the two outstanding mesial edges of the epiotics. The neurocranium of *Dapedium* (B.M.N.H. P 11189) used in the present description is small and probably of a young individual, and the supraoccipital is clearly apparent. Further, a supraoccipital can also be distinguished in a specimen of *Dapedium granulatum* from the Lower Lias of Lyme Regis (G.S. 60122). The neurocranium of *Dapedium* is drawn out dorso-ventrally in the posterior region and the supraoccipital appears to be a fresh development in order to fill in the posterior dorsal apex. Rayner (1948 : 334) has indicated that the supraoccipital in *Aspidorhynchus* and in the Pholidophorid-Leptolepid-Teleost line are not homologous and it is clear that neither of these is homologous with the supraoccipital in *Dapedium* (i.e., the difference in shape, size and extent in all these forms possessing it). In the only other Semionotoid neurocranium known, *Lepidosteus*, the condition is as in *Lepidotes* and the supraoccipital is absent.

Since the Semionotidae have evolved separately from the remainder of the Holostei, the question of the ancestry may be examined. Most authorities have expressed the opinion that there is no known Palaeoniscoid or Subholostean family that approaches that condition found in *Acentrophorus*. Westoll (1944 : 95) in contrast to these believes that there is strong evidence, which he does not publish, for deriving the Semionotids from the Palaeoniscoid family Elonichthyidae.

Elonichthys (Text-fig. 75) comes from the Carboniferous and is related to both *Gonatodus* and *Drydenius*, but differs mainly, as *Rhadinchthys* differs from *Mesopoma*, in the method of jaw suspensions. In *Gonatodus*, *Drydenius* and *Mesopoma* a more vertical suspensorium was acquired. Watson (1925 : 856 ; 1928 : 57) has demonstrated that in *Elonichthys caudalis* changes in the structure of the palate have already started and that the pterygoid has separated from the maxilla dorsally. In so doing the curious tube in which lay the *musculus adductor mandibulae* has disappeared, and, as Watson comments (1925 : 858) : " in this feature they [*Elonichthys*] have reached a condition which is found in all Holostei ". All that is necessary now is for the maxilla to become movable, and the suspensorium to straighten, and a true Holostean state of affairs would be in existence. Simultaneously with this freeing of the pterygoid from the maxilla, a close connection between the metapterygoid and the preopercular and hyomandibular was also established.

Secondly in *Elonichthys* the circumorbital series is represented by a ring of bones numbering eight in *Elonichthys serratus*. These then cannot be identified individually with the ring of five which make up the circumorbital series of the majority of Palaeoniscoids, *Coccocephalus*, *Canobius*, *Mesopoma*, *Rhadinichthys*, etc. Thus we have a Palaeoniscoid with a series of orbital bones much larger in number than is the normal condition in the Palaeoniscoidea ; as Watson comments, " the division of the orbital bones foreshadows that in the Semionotidae ".

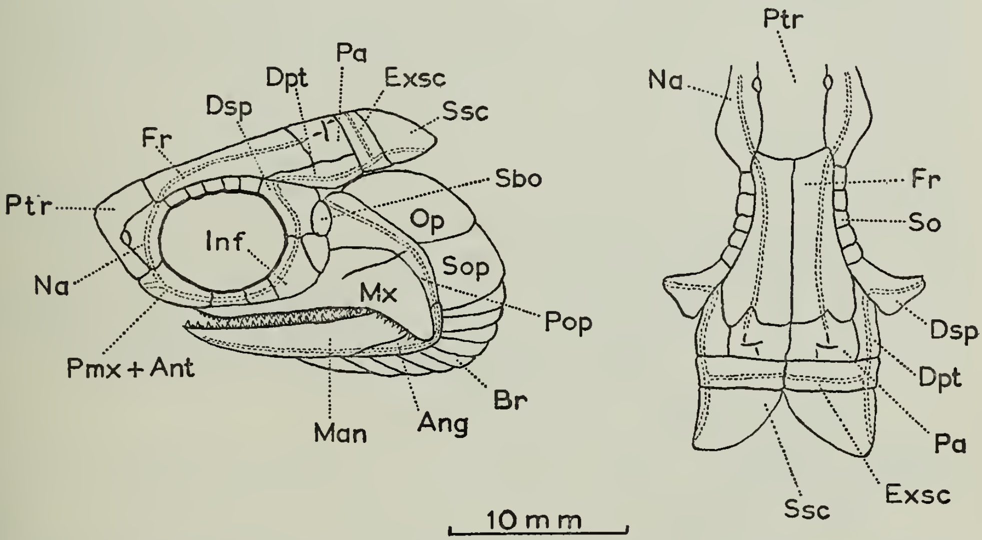

FIG. 75. *Elonichthys serratus* Traquair. Restoration of skull in dorsal and lateral views, from Moy-Thomas & Dyne (1938).

Thirdly, between the posterior circumorbitals and the anterior rim of the preopercular is a series of suborbital bones, three in *Elonichthys caudalis*, two in *Elonichthys serratus* (Text-fig. 75). These could quite easily provide the source for the suborbitals of the Semionotidae.

Fourthly, the supraorbital canal in *Elonichthys caudalis* ends in the frontal and does not pass on into the parietal ; in this respect Watson indicates that it may show a condition intermediate between the normal Palaeoniscoid and that of *Oxygnathus*. In this respect it could also be intermediate between that of the normal Palaeoniscoid and *Acentrophorus*.

Fifthly, *Elonichthys* shows a limited development of ridge scales similar to that condition found in *Acentrophorus*, and lastly, *Elonichthys* still has its full complement of branchiostegal rays, and they are not reduced as in *Mesopoma*.

From the above facts it is clear that although *Elonichthys* is a long way off that grade of organization seen in *Acentrophorus*, it does show changes of the right nature. It is quite unlikely that the family Elonichthyidae is ancestral to the Semionotoidea but until new forms are found (from the Lower Permian) which establish clearer relationships, then as far as can be seen they are about the only family from which the Semionotoidea could be derived.

ASPIDORHYNCHOIDEA

The fourth group of Holosteans to be dealt with, the Aspidorhynchoidea, includes the single family Aspidorhynchidae. This family ranges from the Middle Jurassic to the Upper Cretaceous. In it are included two closely-allied genera, *Aspidorhynchus* and *Belonostomus* (Text-fig. 76). Both these genera are highly specialized on their first appearance, possessing elongated bodies and snouts, and deepened flank scales. In *Aspidorhynchus* the rostrum is produced well beyond the mandibular symphysis, but in *Belonostomus* (Saint-Seine, 1949, fig. 114) the rostrum is only just longer than the mandible. The skull roof in both genera is typically Holostean and there is a dermosphenotic in *Belonostomus tenuirostris*, although Rayner (1941 : 229) indicates that it is missing or fused with the frontals in some species of *Aspidorhynchus*. In contrast the extrascapular is seemingly absent in *Belonostomus*. There is only one series of bones (three in number) between the eye and the preopercular in *Belonostomus*, and these represent the fused suborbitals and posterior infraorbitals, since a sensory canal runs round the anterior rim of the series. The condition of the cheek plates and the preopercular is almost identical to that condition found

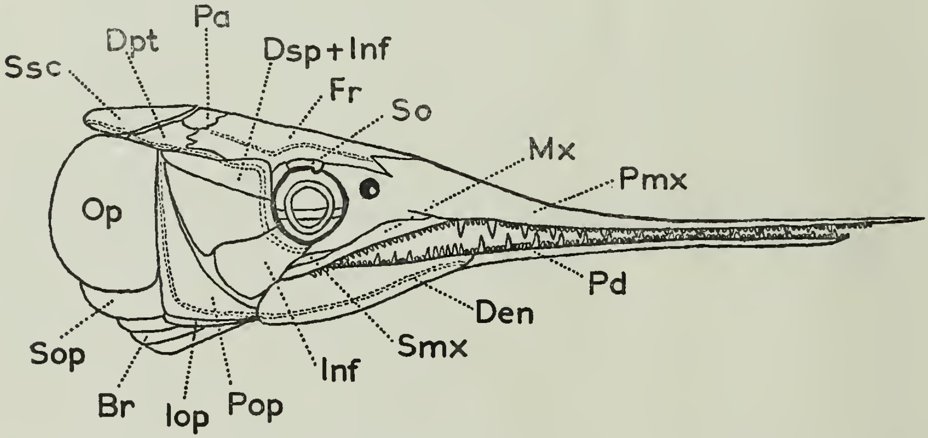

Fig. 76. *Belonostomus tenuirostris* Agassiz. Restoration of skull in lateral view, after Saint-Seine (1949).

in *Pholidophorus*. Other points of similarity between the Aspidorhynchoidea and the Pholidophoroidea include the absence of the basipterygoid process, the similar mobile maxilla with a supramaxilla attached, and the composition of the lower jaw, where in both the surangular is missing.

The neurocrania of the Aspidorhynchoidea and the Pholidophoroidea exhibit several differences. In both there is a supraoccipital, but in the former it is a very small bone and has nothing like the extent of the corresponding bone in the Pholidophoroidea. The intercalar is reduced in the Pholidophoroids, while the lateral occipital stretches round underneath it to form part of the wall in the posterior postorbital region (Text-fig. 74). In the Aspidorhynchids the intercalar is large and constitutes a considerable portion of the wall of the neurocranium in the median postorbital region (Text-fig. 74). In conclusion, the Pholidophorids are peculiar in having an autopterotic in the neurocranium (although as I have already indicated, it is probably homologous with the opisthotic of the Amioids) while the Aspidorhynchids have an opisthotic but this is only present in early ontogeny.

So we see that the Aspidorhynchoidea share a number of characters in common with the Pholidophoroidea, but because of their highly specialized state when they first appear, it is difficult to classify them with the Pholidophoroidea. Westoll (1949 : 95) suspects a relationship between the Aspidorhynchoidea and the Triassic Saurichthyidae and Pholidopleuridae, but both these groups are highly specialized in themselves, and I can see no evidence whatsoever for even the remotest connection.

In the last instance I feel loth to postulate an entirely separate evolution for the Aspidorhynchoidea, so tentatively until new forms are found, I link them with the ancestral Pholidophoroid stock.

PYCNODONTOIDEA

Finally, in the grade Holostei, I include the superfamily Pycnodontoidea. The earliest known Pycnodont, *Eomesodon hoeferi*, comes from the Upper Trias of Hallein, Salzburg, and the family continues until the Eocene when it dies out.

In general organization the Pycnodonts are Holostean and superficially resemble the contemporary Semionotid, *Dapedium*, but this is entirely due to similar modes of life. The appendicular skeleton of the Pycnodont is quite distinct from that of the Palaeoniscoids, but identical to that of the majority of the other Holostei. The fins are unmistakably Holostean with the dorsal and anal fins closely resembling those of *Dapedium*—the rays being equal in number to their supports—and the tail is hemiheterocercal. However, the Pycnodonts show many features which cannot be reconciled with the more conservative Semionotid or Furid condition ; the much expanded preopercular, the unusual pattern of the skull roof with a median supraoccipital and the short Palaeoniscoid-like parasphenoid (Woodward, 1939 : 609). Other respects in which the Pycnodonts differ from the remainder of the Holostei include the unossified vertebral centra, the cheek plates (where present) reduced to tesserae, the almost complete reduction of the branchiostegal rays, the minute fin fulcra and the reduction of scales on the caudal region. Thus the

Pycnodonts must represent a quite separate and independent evolution from other Holostean groups.

A Comparison of the Pycnodonts with the Platysomida

Since the Pycnodonts show no real similarity to any other Holostean family, the question of their ancestry requires examination. Woodward (1939 : 608) considers that the Pycnodonts have been directly derived from the Platysomids. In doing so he assumes that " a highly specialized type of Chondrostean has evidently passed into a still more specialized type of Holostean ". This view is untenable if one considers the well-marked differences between the two groups.

Moy-Thomas & Dyne (1938), Moy-Thomas (1939) and Dyne (1939) have shown that within the Platysomida there are at least two distinct lineages, the Amphicentridae and the Platysomidae. From their evidence it is probable that the Platysomids are polyphyletic in nature, but for convenience in discussion the two families will be treated as one group, the suborder Platysomida, except where otherwise stated.

In the Pycnodonts the roof of the mouth is occupied by the so-called " vomer ", which bears several rows of rounded crushing teeth, which oppose a similar series set on the splenial bone. This formidable dentition is nowhere encountered in the Platysomidae, but is paralleled in several members of the Amphicentridae. The cleithra differ in the two groups (Pycnodonts and Platysomida) and there are no clavicles in the Pycnodonts. The dorsal and anal fins in the Pycnodonts are supported by only one set of radials instead of the two sets in the Platysomida, and the fin-rays in the Platysomida are more numerous than the distal set of radials (or baseosts). Fin fulcra are present in the Platysomida, the branchiostegal apparatus is complete, and the tail heterocercal.

The affinities between the two groups include a persistent notochord, the similarity in the scales and scale distribution, the presence in at least one species of *Platysomus* of a dorsal lateral line besides the median lateral one, the general shape of the head and the prognathic snout. Most of these points were enumerated by Traquair (1879 : 382), but in view of the differences it is impossible to derive the Pycnodonts direct from the Platysomida despite their similarities.

A Comparison of the Platysomida with the Bobasatraniidae

Woodward (1939 : 608) further proposed that partial links between the Pycnodonts and the Platysomida are provided by the Lower Triassic family, the Bobasatraniidae. The Bobasatraniidae do in fact resemble the later Pycnodonts, but could not themselves be direct derivatives of the Platysomida. White (1932 : 83) considered the Bobasatraniidae to be directly derived from the Palaeoniscids rather than from the Platysomids, but following Stensiö (1932) and Lehman (1957) it is more reasonable to assume that the two groups (Bobasatraniids and Platysomids) are closer and that from a basic Platysomid-like stock both the Bobastraniidae and many Platysomids have been evolved. In view of the possible polyphyletic nature of the Platysomida, it is more probable that the Bobasatraniids came from the basal stock of the family Amphicentridae than from that of the Platysomidae.

Similarities between the Bobasatraniidae (Text-fig. 77) and Platysomida include the general shape of the head and body, and the make-up of the shoulder girdle. The two sets of radials supporting the dorsal and anal fins, the axonosts of which are expanded, compressed and sinuous and in contact with one another in both forms (Westoll, 1944). The distribution of the cheek plates is similar and the preopercular has at least two ossifications along the preopercular canal in the Bobasatraniids and in the two Platysomids, *Platysomus gibbosus* (Westoll, 1941 : 47) and *Platysomus parvulus* (Moy-Thomas, 1939, fig. 30*a*). Westoll (1941 : 47) points out the strong resemblances shown in the shape, distribution and ornamentation of the squamation between *Platysomus gibbosus* and *Bobasatrania*. Further, the peculiar development of paired, arcuate tubules from the main lateral line in *Bobastrania* is also found in *Platysomus gibbosus*. In the cheek region the maxillary portion of *Bobasatrania* is easier to associate with that of the family Amphicentridae than it is with the Platysomidae, in both the Bobasatraniids and the Amphicentrids teeth being missing on the maxilla.

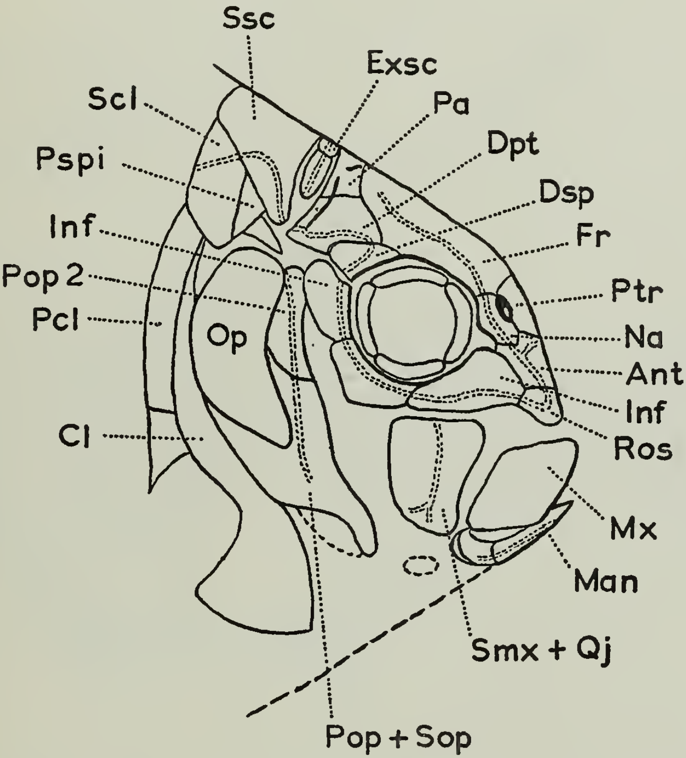

FIG. 77. *Bobasatrania mahavavica* White. Skull in lateral view, after Lehman (1956).

Dissimilarities between the Platysomids and the Bobasatraniids include the

Holostean-like structure of the median fins of the latter. The axonosts and baseosts in the median fins very nearly correspond in number in *Platysomus*, whereas in the Bobasatraniids the baseosts are more numerous than the axonosts and are almost equal to the lepidotrichia. The opercular apparatus is very different in the Bobasatraniids, having a ventral preopercular plate below and beneath the opercular and a much reduced opercular. Other major differences include the complete reduction of the branchiostegal rays in Bobasatraniids and the ventrally broadened cleithrum with no clavicle present.

A Comparison between the Bobasatraniidae and the Pycnodontidae

The Bobasatraniidae and the Pycnodontidae bear many similarities, but the very specialized nature of the former rules out the possibility of a direct descent for the Pycnodonts from the Bobasatraniids, as Woodward (1939 : 608) postulated. However, there is little doubt that both groups originated from the same basic stock.

The similarities between the Bobasatraniids and the Pycnodonts are numerous, and all those features of *Bobasatrania* which are alien to the Platysomids agree with the condition found in the Pycnodonts. The structure of the fins of the Bobasatraniids corresponds with that of the Pycnodonts, and the opercular apparatus is very similar in the two groups. In both there is an almost complete reduction of the branchiostegal rays, and neither group possesses a clavicle. Perhaps the most important similarity between the Bobasatraniidae and the Pycnodontidae so far not mentioned in the literature is the presence of at least two ossifications along the preopercular canal in both families. The present author has shown that the small bone above the preopercular in *Eomesodon liassicus* (Text-fig. 51) carries a portion of the sensory canal and therefore must be considered as a preopercular plate. This division was also seen (with the canal) in *Mesodon macropterus* and *Coelodus costae*.

Other similarities between the Bobasatraniidae and Pycnodontidae include a backwardly-inclined hyomandibular, devoid of an opercular process. [However, Woodward (1895*b* : 193) records an opercular process for *Gyrodus* in a position similar to that of the other Holostean groups and to the Teleosts.] Again the hyomandibular articulation is identical, there being a symplectic between the hyomandibular and the quadrate in both groups and there seems to be some provision for movement between the symplectic and the quadrate, a condition also observed in *Dorypterus*. The courses of the sensory canals are very similar on the head bones of the Bobasatraniidae and the Pycnodontidae, and are in all essentials of the Palaeoniscoid-Platysomid type in both. The lateral line of the Pycnodonts still retains the ventral tubule of the arcuate pair (Text-fig. 53) and has a dorsal division similar to that of the Bobasatraniids and some Platysomids. There are large ridge scales in front of the dorsal and ventral angles in both the Pycnodonts and Bobasatraniids. The shape and structure of the scales are similar, both forms having scales higher than broad, with well-developed peg-and-socket articulations. The scales are characterized by their rhombic shape and by a fairly strong ridge on the anterior part of the median side. The lepidotrichia of the Bobasatraniids become rather separate and resemble more closely the condition found in the Pycnodonts rather than that found in the Platysomids. An unusual post-abdominal bone is found in the Bobastraniids and in some Pycnodonts (e.g. *Gyrodus frontalis*), but this bone also occurs in the Platysomids and in *Dorypterus*. The mandibles of the two groups are not so alike, and Dunkle & Hibbard (1946) have shown that the mandible of *Micropycnodon* is more like that found in the Platysomids than in the Bobasatraniids.

Other peculiarities of the Bobasatraniids include an increase in size of them axilla and premaxilla, the former being absent in the Pycnodonts and the latter reduced, the loss of the pelvic fins and the presence of a more or less complete squamation. The axial and fin skeletons are also different ; in the Pycnodonts the neural and haemal spines are joined to the neural arches and there is but a single row of fin supports. Westoll (1941 : 48) suggested that these last differences " may be due to the structural needs of the developing fish ", and this probably applies to the scales as well. These and other differences point to the fact that the Pycnodonts could not have been directly derived from the Bobastraniids, but most probably came from the same Palaeoniscoid stock, the same stock that gave rise to the Amphicentridae.

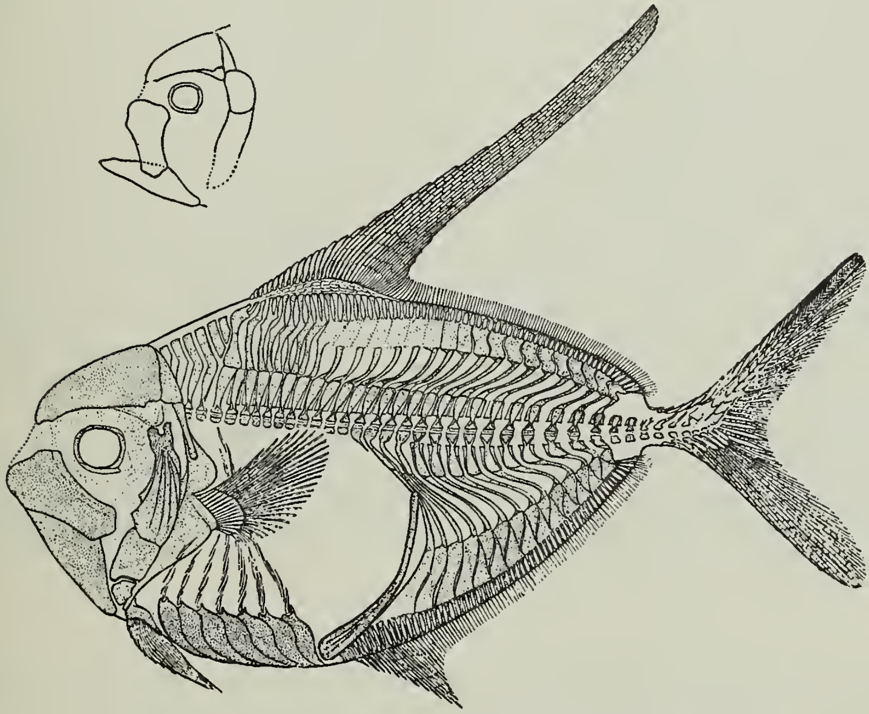

FIG. 78. *Dorypterus hoffmani* Germar. From Gill (1925).

Summing up all the evidence, it is clear that from a Platysomid-like ancestral stock both the Amphicentrids and the Bobastraniids evolved. The line leading to the Bobasatraniids later dividing to give on the one hand the Bobasatraniidae and on the other the Pycnodontidae (Text-fig. 79).

Dorypterus *Compared with the Bobasatraniids, Platysomids and Pycnodonts*

Mention must be made of another closely-allied genus, *Dorypterus* (Text-fig. 78). There are close relationships between the axial skeleton and fin skeleton of *Dorypterus* and *Bobasatrania* (e.g. the expanded, sinuous axonosts in contact with one another in both genera), and in the development of the body axis of the caudal fin. The heterocercal tail is modified by a thinning and weakening of the body lobe in *Bobasatrania* and is similar to the condition found in *Dorypterus* (Westoll, 1941 : 42). The bones of the upper jaw are similarly developed in both, and the pectoral girdles show many likenesses. Despite these few similarities there are many divergent features ; no known Bobasatraniid, or Platysomid for that matter, shows the extreme modifications of the skull found in *Dorypterus* (Gill, 1925 : 643 ; Westoll, 1941 : 39). Likewise, the body of *Dorypterus* is not completely covered with thick scales as in the Bobasatraniids or Platysomids. The scaling is reduced to the anterior portion of the trunk, and in this respect *Dorypterus* resembles the Pycnodonts. Westoll (1941 : 48) describes the condition found in the Pycnodont *Mesodon* and points out the close similarity between the nature and the extent of the scaling of it and *Dorypterus*. He also points out that the presence of additional scales on the caudal lobe of *Dorypterus* is paralleled by similar scales on the reduced caudal lobes of *Microdon* and *Mesodon* (noted by Woodward, 1918 : 52, 64). However, these features, as Westoll correctly recognized (1941 : 48), do not prove a close relationship between the Pycnodonts and *Dorypterus*, since they are probably concerned with similar adaptations in the two forms (e.g. reduction in body weight, stabilization in the vertical plane).

From the evidence it is clear that *Dorypterus* is much more closely related to the Platysomids and the Bobasatraniids than to the Pycnodonts. The Dorypterids and Bobasatraniids must have come from the same early Platysomid-like stock, the two lines diverging, the Bobasatraniid line eventually giving rise to both the Bobasatraniids and the later Pycnodonts, whilst the Dorypterid line soon died out.

IV. CONCLUSIONS

From the previous discussion it is clear that the Holostei do not form a natural order but include families derived from different Palaeoniscoid stocks. These derivatives happen to share similar but independently acquired characters, such as construction of the cheek, opercular apparatus, fins, appendicular skeleton and the reduction of the heterocercal tail. Many of these characters have also been independently acquired by several other groups which do not quite reach the Holostean grade of evolution (e.g. *Ptycholepis*, *Haplolepis*, *Aeduella*), but which come under Brough's (1936, 1939) category of Subholostei.

Both the orders Holostei and Subholostei include forms derived from different Palaeonisciform stocks, and as such represent grades of evolutionary development rather than natural, monophyletic orders. Therefore the retention in the classification of the orders Subholostei and Holostei should be abandoned, since not only do they cut across phyletic lines but, as Westoll (1944 : 96) states, " they are based on characters which are of adaptational nature ". In this respect I agree with

Westoll and his work may be consulted for further discussion on the subject. In spite of abandoning the status of the two groups as orders, the terms " Holostei " and " Subholostei " can for the time being at least be usefully retained for convenience in discussion, for although purely arbitrary they have become through general usage associated with a certain grade of organization.

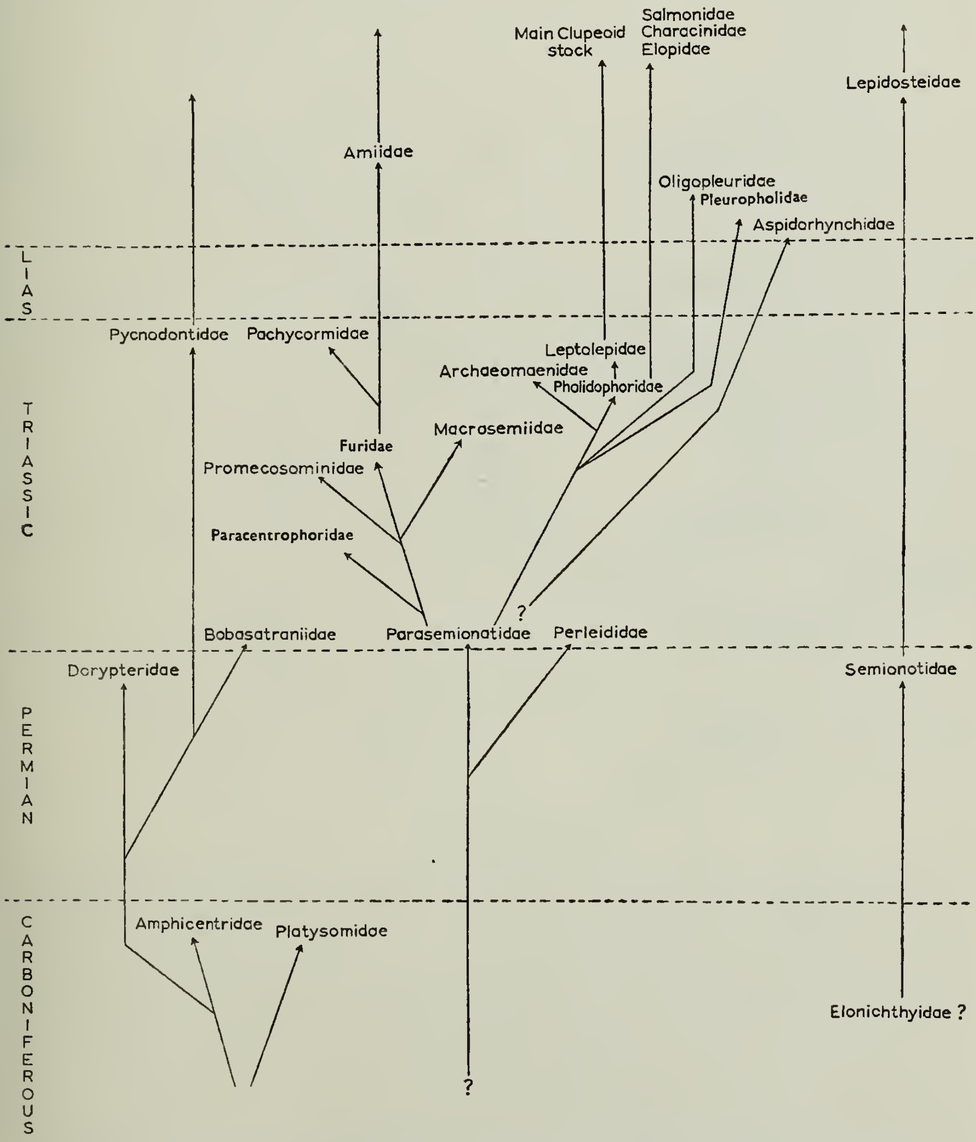

FIG. 79. Evolutionary tree of the main Holostean groups.

In conclusion, the arrangement of the families included in the term Holostei by previous authors is set out below and superfamily designation is given to the individual groups.

" HOLOSTEI "

Group I. Amioidea

- i. Furidae.
- ii. Amiidae.
- iii. Macrosemiidae.
- iv. Pachycormidae.
- v. Promecosominidae.
- vi. Paracentrophoridae.

Group II. Pholidophoroidea

- i. Pholidophoridae.
- ii. Leptolepidae.
- iii. Oligopleuridae.
- iv. Pleuropholidae.
- v. Archaeomaenidae.
- vi. Protelopidae.

Group III. Aspidorhynchoidea

- i. Aspidorhynchidae.

Group IV. Semionotoidea

- i. Semionotidae.
- ii. Lepidosteidae.

Group V. Pycnodontoidea

- i. Pycnodontidae.

" SUBHOLOSTEI "

This term embraces a variety of forms which resemble the Palaeoniscoids, but which also show various progressive structural trends towards that grade of organization termed Holostean. The order Subholostei, as I have already indicated, should be abandoned, since it is essentially a horizontal classification, but the retention of the term Subholostei is necessary for the time being at least, for ease in discussion.

Three of the genera I have described from the Lower Lias of Lyme Regis come within the meaning of the term Subholostean, in that they all show developments from the Palaeoniscoid condition towards the Holostean one.

The first genus described is *Platysiagum*, which is placed in the family Platysiagidae. *Platysiagum* is the single genus and contains the Middle Triassic species *Platysiagum minus* (Brough, 1939 : 14) and the Lower Liassic *Platysiagum sclerocephalum* (Text-fig. 13). Brough (1939 : 17) has already pointed out that this genus, although superficially Palaeoniscoid, has departed in many respects from the Palaeoniscoid plan. The paired fins and the hemiheterocercal tail are distinctly Holostean in nature, while the lower jaw has a pronounced coronoid process on it. There is an incipient interopercular, the suspensorium is upright and the maxilla partly freed from the preopercular. The affinities of the family are vague, there being no other Subholostean or Holostean with which it could be linked. As Brough (1939 : 17) concludes, it is merely the representative of another Palaeoniscoid line which has moved independently towards the Holostean grade of structure.

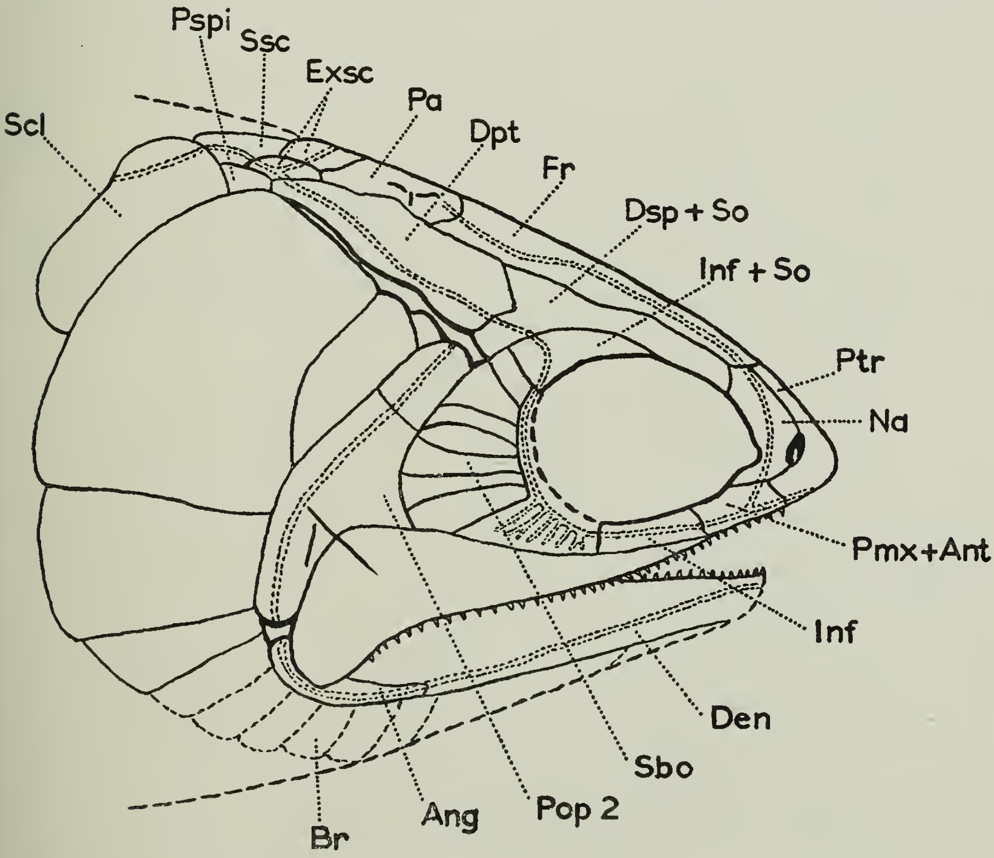

FIG. 80. *Boreosomus gillioti* Priem. Lateral view of skull, after Lehman (1952).

The second genus dealt with is *Ptycholepis*. This genus had for a long time been considered Holostean and placed in the Furidae (Eugnathidae, Woodward, 1895*b*: 316). However, the works of Brough (1939 : 98) and Aldinger (1937) have shown that *Ptycholepis* is not a Holostean, and that it must be regarded as the representative of yet another independent line from the Palaeoniscoids. Both these authors agree that the Ptycholepids have been derived from the Palaeoniscoid *Boreosomus* (Text-fig. 80), with which they share many points of similarity.

The earliest Ptycholepid is *Ptycholepis barboi* (Brough, 1939 : 58) from the Middle Trias of Besano. I have redescribed the Lower Lias species *Ptycholepis monilifer* and the Upper Liassic *Ptycholepis bollensis*. In *Ptycholepis bollensis* (Text-fig. 17) the sensory canal system of the head was well shown, and the true homologies of the postorbital bones recognized. These postorbital bones clearly represent the posterior infraorbitals which have grown back over the preopercular, since the infraorbital sensory canal passes through their anterior edges. Moreover, the small bone termed a supramaxilla by Brough (1939, fig. 30) is in fact a member of the infraorbital series, since through it also the infraorbital canal passes.

The third and last genus described is *Saurorhynchus*. It belongs to the family Saurichthyidae, which according to Stensiö (1925 : 175) contains two genera, the first *Saurichthys*, into which all the Triassic forms are placed, and the second *Saurorhynchus*, which embraces the two Liassic species *Saurorhynchus acutus* (Agassiz) and *Saurorhynchus brevirostris* (Woodward). Stensiö (1925 : 175) states that *Acidorhynchus* (*Saurorhynchus*) differs from *Saurichthys* in the following respects :

> " (1) Smaller lengthening of the rostrum.
> (2) No or very slight ganoine ornamentation.
> (3) Certain differences in the shape and relations of the dermal bones.
> (4) Rather much reduced opercular.
> (5) Absence of vertical striations on the teeth basally of the enamel cap."

One further difference, according to both Woodward (1895*b* : 10) and Stensiö (1925 : 176) is the ossification of the neurocranium, which in *Saurorhynchus* is degenerate and cartilaginous.

Most of these differences have now been shown to be invalid. The first, " the smaller lengthening of the rostrum " is incorrect, because from a series of measurements made on all the Saurichthyids and Saurorhynchids in the B.M.N.H. the resultant graphs (Text-fig. 81) and calculations showed that there was no significant difference in the relative length of the rostrum in *Saurichthys* and *Saurorhynchus*. The second difference, " no or very slight ganoine [enamel] ornamentation ", is also invalid, several specimens of *Saurorhynchus* having skull bones distinctly ridged and tuberculated with enamel. The third difference noted by Stensiö, " the differences in the shape and relations of the dermal bones " is, however, correct, the maxilla and preopercular in particular being quite distinct in shape and size. The rather reduced opercular is also a recognizable difference, the opercular rarely extending far below the ventral limit of the preopercular. However, the " absence of vertical striations on the teeth basally of the enamel cap " is incorrect, for on some teeth of *Saurichthys* these striations are absent, whilst on others of *Saurorhynchus* they are present (Text-fig. 22). Lastly, the neurocranium is ossified in *Saurorhynchus*, although not so heavily as in the earlier Saurichthyids. The neurocrania differ in one or two respects : the cranio-spinal process is not so wing-like in *Saurorhynchus* as in *Saurichthys*, the myodome not so deep and the parasphenoid extends much further forward along the base of the rostrum than in *Saurichthys*.

These differences are sufficient for separating the Liassic species, *S. acutus* and *S. brevirostris*, from the remainder of the Saurichthyids, and for putting them in a separate genus, *Saurorhynchus*, as Stensiö (1925 : 175) proposed.

The relationships of the Saurichthyidae have been exhaustively dealt with by Stensiö (1925 : 207) and it only remains for me to emphasize that they form a

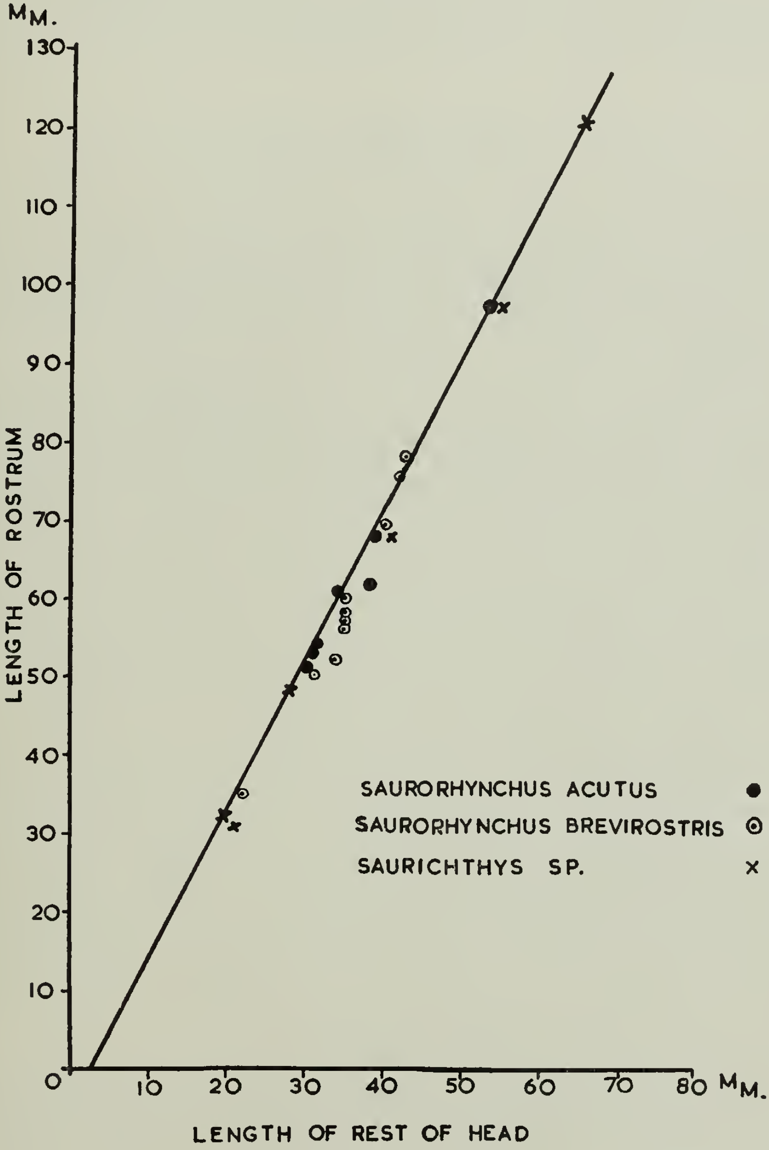

Fig. 81. Graph of length of rostrum against length of rest of head.

degenerating series closely related both to the Palaeoniscoids and to the Sturgeons (Acipenserids, Chondrosteids and Polydontids).

In conclusion, mention must be made of the genus *Browneichthys*. This genus is known from one fragmentary fossil from the Lower Lias of Barrow-on-Soar, Leicestershire, and now in the Leicester Museum. Woodward (1895*b* : 23) provisionally associated it with the Saurichthyids under the name of *Browneichthys ornatus*. From its unique scale pattern I find it difficult to classify it with the Saurichthyids, a view already put forward by Griffith (1958 : 159).

PALAEONISCOIDEA

The Palaeoniscoids have an exceedingly long range in the geological time scale, extending from the Middle Devonian until the Cretaceous. During that time many of the lines developed independently towards the Holostean grade of organization. However, one or two of the families were more conservative in nature, and retained the Palaeoniscoid structure practically unaltered right through until the Jurassic and Cretaceous.

One such family is the Coccolepidae. This family contains the single genus *Coccolepis* and ranges upwards from the Lower Lias (*Coccolepis liassica*) to the Wealden of Belgium (*Coccolepis macroptera*). In addition it has a very wide geographical distribution, members of the genus being recorded from England, Belgium, Turkestan, Russia and New South Wales. It contains the last members of the Palaeoniscoidea and culminates in the Lower Cretaceous. The Lower Liassic species *Coccolepis liassica* shows little advance in structure over such Devonian forms as *Cheirolepis* and *Stegotrachelus*. It still retains a very oblique suspensorium and there is no suborbital series developed, but the nasal region has become a little modified by the loss of the overhanging rostrum and the formation of a premaxilla.

Another genus from the Lower Lias of Lyme Regis is *Centrolepis*. It contains the single species *Centrolepis aspera*, which previously was placed provisionally first in the Palaeoniscoidea by Woodward (1891 : 520) and then in the Palaeoniscoidea or Subholostei *Incertae Sedis* by Romer (1945 : 580). From my description there is no doubt that the genus correctly belongs with the Palaeoniscoidea. The structure and disposition of the skull roofing bones are very similar to that condition found in *Rhadinichthys* (Lower Carboniferous). Apart from the absence of a " dermohyal " in *Centrolepis aspera*, the remainder of the skull is strikingly similar, including the two suborbitals, the opercular apparatus, the make-up of the pectoral girdles and the cheek and snout regions. *Centrolepis* is very much larger than *Rhadinichthys*, being almost three times as long, and it has several peculiarities including the branching of the sensory canal system anteriorly. The normal Palaeoniscoid condition is for the infraorbital canal to branch in the rostral bone and give off an anterior branch that passes into the postrostral. In *Centrolepis aspera* (Text-fig. 5) the infraorbital canal does not branch until it is in the nasal bone. Added to this is the distinct nature of the scales and the relative position of the fins. From these differences it is obvious that the Centrolepids represent a rather isolated lineage and there is every cause for placing the genus *Centrolepis* in a family of its own, the Centrolepidae.

The remaining Palaeoniscoid from the Lower Lias of Lyme Regis is *Oxygnathus*. This genus has been more or less completely described by Woodward (1890 : 431) and Watson (1925 : 867 ; 1928 : 58). It has been correctly placed by Romer (1945 : 579) in the family Palaeoniscidae, and bears many similarities with earlier members of this family. Such forms as the Triassic *Glaucolepis* and the Permian *Palaeoniscus* are quite comparable with *Oxygnathus* in general structure of the skull and make-up of the body.

The three Liassic Palaeoniscoids described all represent end lines which have managed to survive comparatively unchanged from the Palaeozoic, and which eventually succumb to the far better adapted Holosteans and Teleosts.

COELACANTHIFORMES

The Coelacanthidae range from the Lower Carboniferous to the present. Woodward (1891 : 398) showed that the skeletal characters exhibit little variation; and that " it is difficult to recognize differences sufficiently marked to be regarded as justifying the subdivision of the family into a series of genera ". He points out that the arrangement and proportions of the fins are practically constant, and that the supplementary caudal is the only variable element.

Stensiö (1921 : 119) agrees with Woodward, although he states that there is a rather greater variability than we have been inclined to think, and also that the general characters as a rule are somewhat more strongly marked than was thought to be the case by a number of authors.

The genus I have described from the Lower Lias of Lyme Regis is *Holophagus gulo*, and it is a large fish with a prominent supplementary caudal fin. The isolated pterygoid-quadrate plates described from the Stonesfield Slate are doubtfully of *Holophagus* but their structure shows a considerable amount of variability.

V. ACKNOWLEDGMENTS

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LETTERING USED IN TEXT-FIGURES

a, a_1, a_2 } processes on the ossified primary girdle plate.
Ang, angular.
Ant, antorbital.
Ant.+ Ptr. antorbito-postrostral.
aort, canal for dorsal aorta.
Ap, autopterotic.
ap, anterior pit line.
Art, articular.
asc. ps, ascending process of parasphenoid.

B, basioccipital.
Bbr I, basibranchial I.
Bbr II, basibranchial II.
Bhy, basihyal.
bpt. pr, basipterygoid process.
Br, branchiostegal ray.
Bsph, basisphenoid.

can.W, canals of Williamson.
Cbr. I, ceratobranchial I.
Cbr II, ceratobranchial II.
Cbr III, ceratobranchial III.
Cbr IV, ceratobranchial IV.
Chy, ceratohyal.
Cl, cleithrum.
Clav, clavicle.
Co.pr, coronoid process.
Cor, coronoid.
Cora, coracoid.
Crpsph, crista on parasphenoid.
c.sp, cell space.

d, depression.
Den, dentary.
Despl, dentalo-splenial.
d.l.l,. dorsal lateral line.
Dpt, dermopterotic.
Dpt+Exsc, dermopterotic-extrascapular.
Dsp, dermosphenotic.
Dsp + Inf, infraorbito-dermosphenotic.
Dsp+So, supraorbito-dermosphenotic.
d.t, dentinal tubule.

E, epiotic.
e, enamel (ganoine).
Ectpt, ectopterygoid.
eff.ps.art, efferent pseudobranchial artery.
Enpt, entopterygoid.
Excl, extracleithrum.
Exsc, extrascapular.
ext.car, foramen for external carotid artery.
ext.sc, external semicircular canal.

f, foramen.
f.a, articulatory facet.
fac.art.pal, articulatory surface for the autopalatine.
fac.f, facial foramen (recess).
fh, fenestra hypophyses.
f.hym, facet for hyomandibular.
f.m, foramen magnum.
f.na, facet for neural arch.
Fr, frontal.
fuls, fulcral scale.

Gu, gular plate.

Hbr I, hypobranchial I.
Hbr II, hypobranchial II.
Hbr III, hypobranchial III.
Hbr IV, hypobranchial IV.
hc, supramaxillary sensory line.
Hhy, hypohyal.
h.la, horizontal bone lamellae.
hsp, haemal spine.
Hym, hyomandibular.

I, intercalar.
Inf, infraorbital.
infc, infraorbital sensory canal.
Inf+So, infraorbito-supraorbital.
int.car, foramen for internal carotid artery.
Iop, interopercular.
Ir, interrostral.

L, lateral occipital.
lc, cephalic division of main lateral line.
Lep, lepidotrichia.
l.l, lateral line.

Man, mandible.
mc, mandibular sensory canal.
m.cor.arch, mesocoracoid arch.
Meck, ossified Meckelian cartilage.
Metpt, metapterygoid.
Mix.t, mixicoronoid teeth.
mp, median pit line.
Mssc, median suprascapular.
Mx, maxilla.
myod, myodome.

n_1, anterior nasal aperture.
n_2, posterior nasal aperture.
*N*a, nasal.
Na + Ant, nasalo-antorbital.
nc, neural canal.
not, notochordal pit.
ns, neural spine.
nt, aperture for notochord.
Nu, neural arch.

o, opisthotic
o, pore.
occ.n, foramen for occipital nerve.
Op, opercular.
op.pr, opercular process.
Orb, orbit.
orp, postmaxillary sensory line.
Orsp, orbitosphenoid.
Oss.Prg, ossified primary pectoral girdle.

P, prootic.
p, parapophysis for rib.
Pa, parietal.
Pa+Dpt, parieto-dermopterotic.
Pal, palatine.
Pcl, postcleithrum.
Pd, postdentary.
Pmx, premaxilla.
Pmx+Ant, premaxillo-antorbital.
Pmx-Ros, rostralo-premaxillary.
Po, postorbital.
Po.inf, postorbito-infraorbital bone.
Pop, preopercular.
popc, preopercular canal.
Pop.Po, preoperculo-postorbital.
Pop.Quj, preoperculo-quadratojugal.
Pop+Sop, preoperculo-subopercular.
por, postorbital process.
pp, posterior pit line.
Ppg, primary pectoral girdle.
Pra, preangular.
Prcs, cranio-spinal process.
prof, foramen for profundus.
Psph, parasphenoid.
Pspi, postspiracular.
Pt, pterygoid.
Ptr, postrostral.
Ptsph, pterosphenoid.
Pvg, pelvic girdle.

Qu, quadrate.
Quj, quadrato-jugal.

Ra, radials.
ram.dors, foramen for branches of the ramus ophthalmicus superficialis trigemini.
ros, rostral.
r.ot, foramen for the ramus oticus.
r.s, ridge scale.
Rsc, dorsal ridge scute.

Sang, surangular.
Sbo, suborbital.
s.br, side branches.
Sc, scale.
s.c, sensory canal.
Scap, scapula.
Sc.f, scapular foramen.
Scl, supracleithrum.
Scom, supratemporal commissure.
Scr, sclerotic ring.
Smx, supramaxilla.
Smx+Qj, supramaxillo-quadratojugal
So, supraorbital.
soc, supraorbital sensory canal.
Socc, supraoccipital.
Sop, subopercular.
Sp, splenial.
Spt, suprapterygoid.
Ssc, suprascapular.
Sty, stylohyal.
Sym, symplectic.

$\left.\begin{matrix}t_1\\t_2\\t_3\end{matrix}\right\}$ teeth of lower jaw.
tem.gr, temporal groove.
trig.fac.ch, trigemino-facialis chamber.

vas, vascular groove.
v.can, horizontal network of canals.
vert. cart. ant, vena cerebralis anterior.

Vo, vomer.
Vo.t, vomerine teeth.
v.t, ventral tubule.

w, widening of lateral line.

$\left.\begin{matrix}x_1\\x_2\end{matrix}\right\}$ bones of opercular series.

I, olfactory canal.
II, optic foramen.
III, foramen for oculomotor nerve.
IV, foramen for trochlear.
V, foramen for trigeminal nerve.
V.VII.op.sup, foramen for superficial ophthalmic branches of trigeminal and facial nerves.
VI, foramen for abducens.
VII, foramen for facial nerve.
VII.hym, foramen for hyomandibular branch of facial nerve.
VII.buc, foramen for buccal branch of facial nerve.
VII.pal, foramen for palatine branch of facial nerve.
VII. ot, foramen for otic branch of facial nerve.
IX, foramen for glossopharyngeal nerve.
IX.st, foramen for supratemporal branch of glossopharyngeal nerve.
X, foramen for vagal nerve.

B.M.N.H., British Museum (Nat. Hist.)
G.S., Geological Survey Museum.
Ox. M, University Museum, Oxford.
R.S.M., The Royal Scottish Museum, Edinburgh.
Sedgw. M., Sedgwick Museum, Cambridge.

PLATE 36

Ptycholepis monilifer Woodward

Block 1, showing lower jaw and ceratohyal. B.M.N.H. 39868.

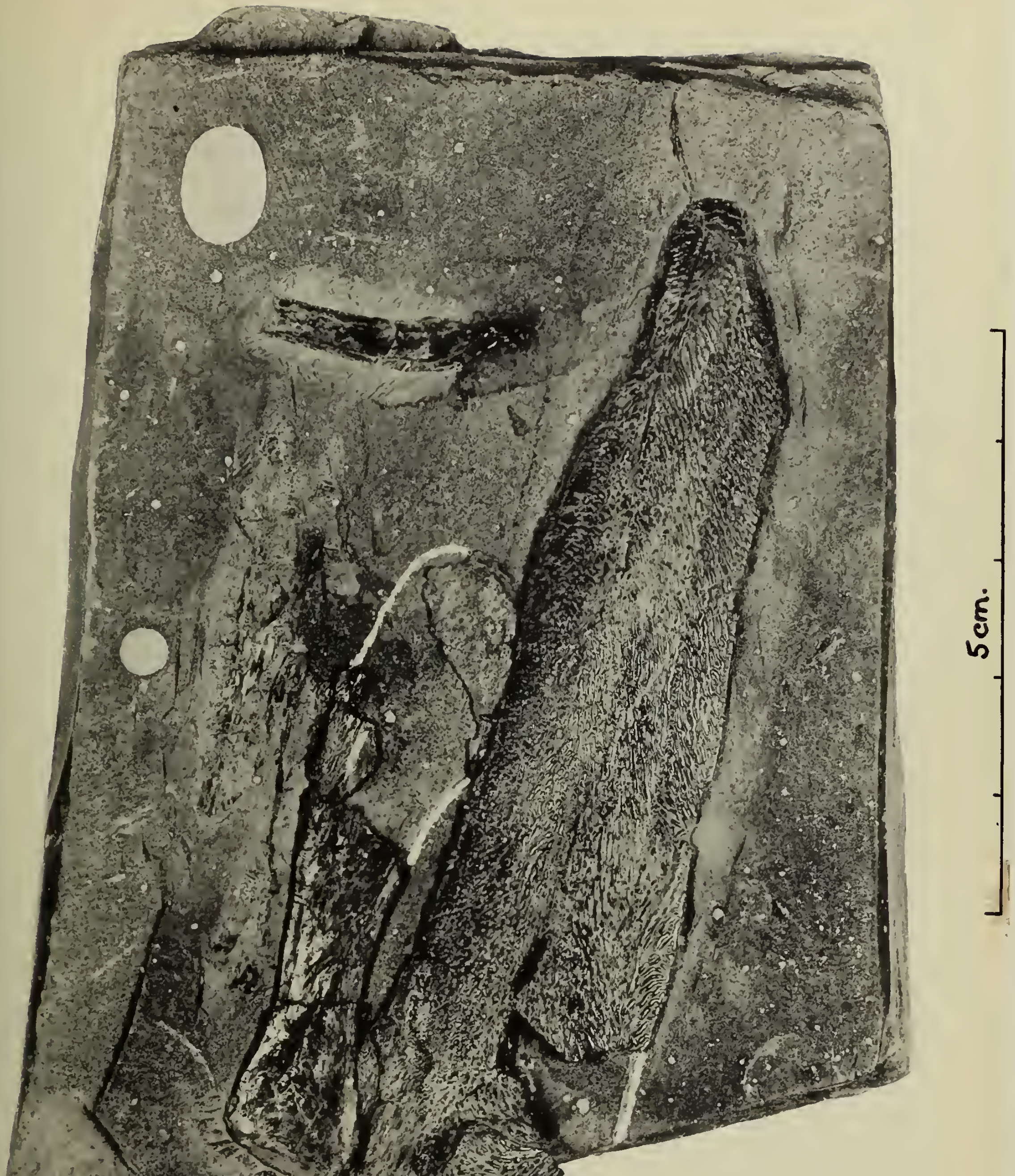

5cm.

PLATE 37

Ptycholepis monilifer Woodward

Block 2, showing maxilla and branchiostegal rays. B.M.N.H. 39868.


5 cm.

PLATE 38

Ptycholepis monilifer Woodward

Block 3, showing preopercular and dorsal fin. B.M.N.H. 39868.

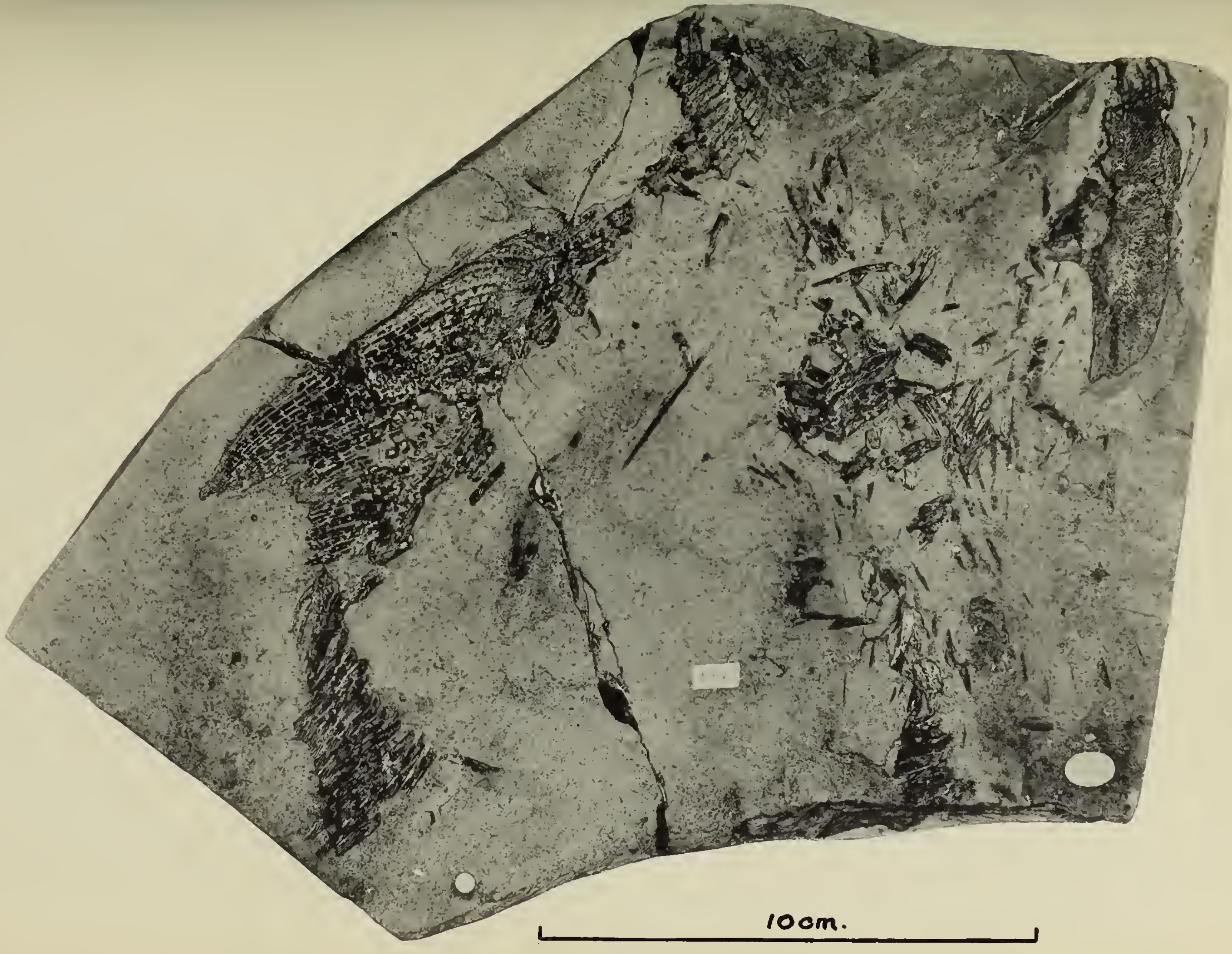

10cm.

PLATE 39

Ptycholepis monilifer Woodward

Block 4, showing tail. B.M.N.H. 39868.

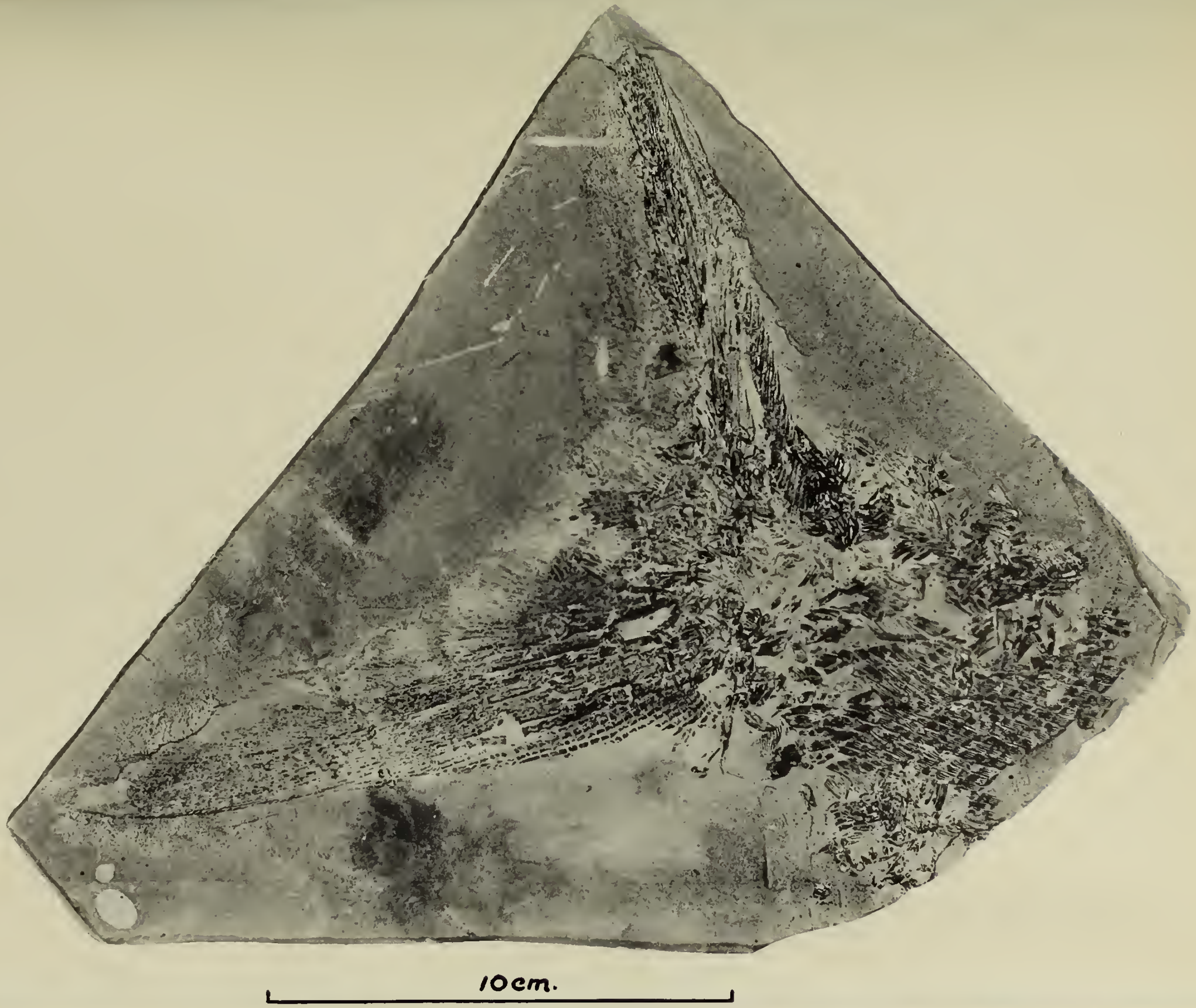

10cm.

PLATE 40

Ptycholepis monilifer Woodward

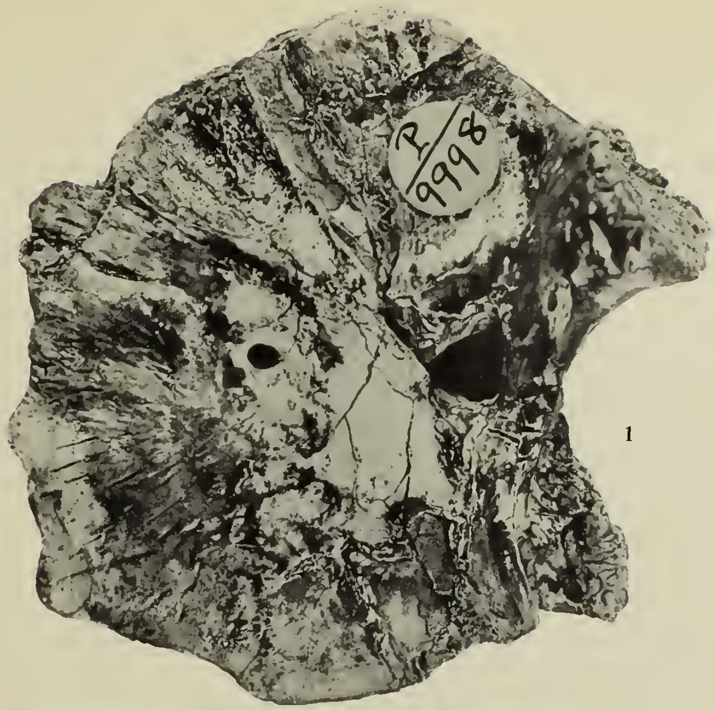
Block 3, portion of scaling. B.M.N.H. 39868. ×4·1.

PLATE 41

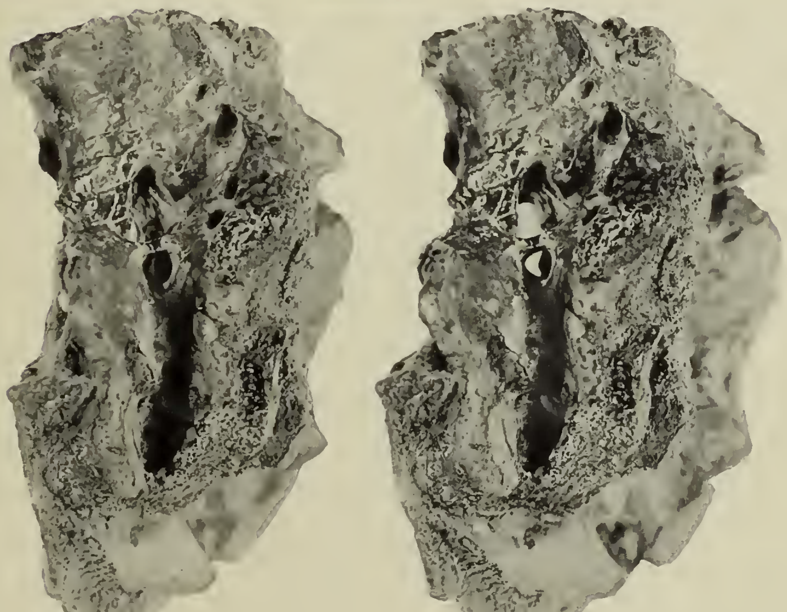
Lepidotes latifrons Woodward

FIG. 1. Right prootic in lateral view B M.N.H. P 9998, scale in mm.

FIG. 2. Stereoscopic photograph of the orbital surface of the right prootic. B.M.N.H. P 9998, scale in mm.



1



2

5mm

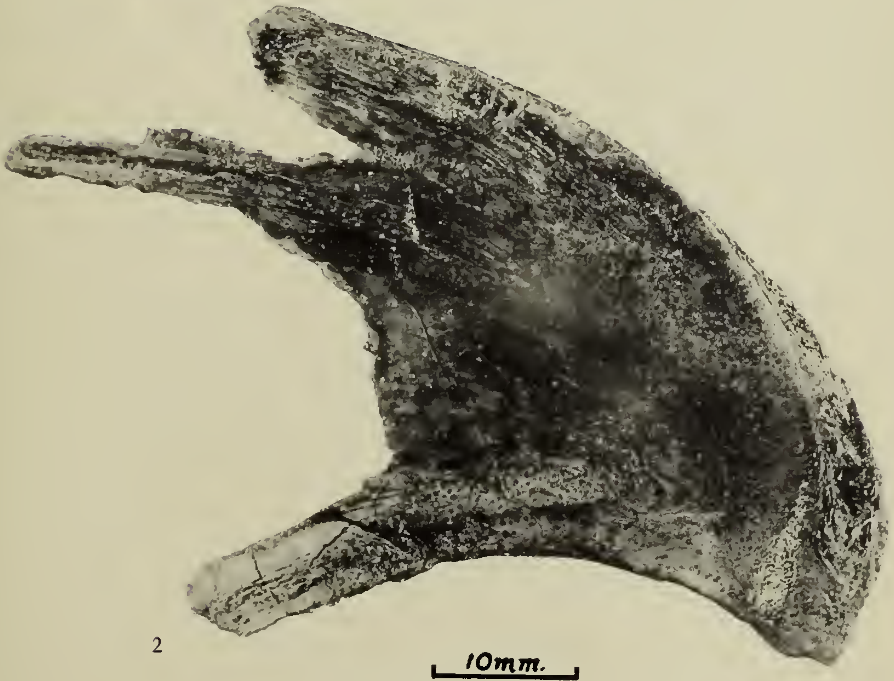
PLATE 42

Holophagus gulo Egerton

FIG. 1. Pterygo-quadrate of right side, outer view. B.M.N.H. P 9842, scale in mm.

FIG. 2. Pterygo-quadrate of right side, inner surface. B.M.N.H. P 9842, scale in mm.

1



2

PLATE 43

FIG. 1. Pterygo-quadrate of an undetermined Coelacanth. B.M.N.H. P 959.

Holophagus sp.

FIG. 2. Gular plate, ventral view. B.M.N.H. P 4277*a*.

1

2